5-2002

Population ecology of black bears in Great Smoky Mountains National Park

Thomas H. Eason
University of Tennessee

To the Graduate Council:

I am submitting herewith a dissertation written by Thomas H. Eason entitled "Population ecology of black bears in Great Smoky Mountains National Park." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

Michael R. Pelton, Major Professor

We have read this dissertation and recommend its acceptance:

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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and recommend its acceptance:

Accepted for the Council:

Vice Provost and Dean
Of Graduate Studies

POPULATION ECOLOGY OF BLACK BEARS IN GREAT SMOKY MOUNTAINS NATIONAL PARK

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Thomas H. Eason

May 2002

DEDICATION

This dissertation is dedicated to my family, whose patience and support have sustained me throughout the course of this dissertation and my life. Especially, I dedicate this work to my Grandparents, Dorothy Ball Eason and Thomas Dotterer Eason, Jr., and to my nephew, Patrick Scott Eason, Jr. My grandparents have grounded me with the traditions and wisdom of the past, while Patrick has filled me with the wonder of youth and things to come.

ACKNOWLEDGMENTS

My work as a graduate student has not been performed in isolation; rather, it has been completed with the hard work, help, and guidance of many people. First, I thank my committee for their ideas, suggestions, and corrections throughout my doctoral program. Without my major advisor, Dr. Mike Pelton, I would not have had the opportunity to continue my study of a most fascinating animal, the American black bear. Thank you, Dr. Pelton, for having the faith to hand me such a large project, full of so much potential. I also thank my other committee members, Dr. Joe Clark, Dr. Dave Etnier, and Dr. Mark Kot, for the generous giving of their time, resources, and energies. It has been a pleasure working with each of you.

The number of people that have shared their graduate education with me is large, and I have enjoyed working with all of them. To my fellow Peltonites: Donny Martorello, Bob Inman, Rich Beausoleil, Jay Clark, Daron Barnes, Alex Coley, Clint Cagle, Todd Allen, Meghan Carr, Don Anderson, Marty Stratman, and Joe Folta, I thank you all for your camaraderie, insights, and friendship. I will always remember our lunchtime discussions at Vic and Bill's, Schlotzki's, Steffanos, and every other eating establishment near campus. May we all keep the faith and remain strong in our day-to-day struggles with the "real world". I give special thanks to Donny Martorello for his never-ending energy and constant support throughout my doctoral career. As always, Frank van Manen was there to lend support, offer ideas, and critique manuscripts. His selfless donation of time and input will always be remembered. I also acknowledge the

contributions of all the other graduate students, both in Forestry, Wildlife, and Fisheries and Ecology, who have taken the time to help out with "the bear work".

The field work for my dissertation took 5 years, and, although it was rewarding in its own right, it was hard work and took the dedication of many people. Alex Coley deserves special recognition as the founder of the North Carolina study area and as an integral member of the initial years of trapping and data collection. Data were collected with the help of many technicians, all of whom worked under severe field and spartan living conditions: Chad Pelton, Heath Smith, Bob Inman, Rick Eastridge, Marcus Spicer, Will Headrick, Clint Cagle, Joe Crews, Brandon Viars, Bryan Riley, Todd Allen, Andy Edwards, Jason Williams, Josh Campbell, Ole Opseth, and Andreas Norin y'all were great. Your long hours of work are appreciated, but, more importantly, your eagerness to sacrifice for the project and your friendship are what I will remember most. Jay Clark and Laura Hiser, both of whom performed admirably under difficult conditions, conducted exploratory camera fieldwork. Later, Sam Murry added a year of data to the camera work with much improved equipment and techniques. Countless other friends, relatives, students, teachers, and interested persons helped with various aspects of the fieldwork, and all are appreciated.

I acknowledge the National Park Service for supporting this work and providing a wonderful study area. Great Smoky Mountains National Park was an ideal setting for studying black bears and I thank everyone there who helped make the work a success. Special thanks go to Kim Delozier and Bill Stiver for promoting the project and lending support whenever it was needed. Richard Jenkins, Glenn Martin, and Dale Raxtor

showed me about and were always excited to help out. I also thank Morristown Aviation for the countless hours of radio telemetry flights. The adept flying of Bob Shoun and David Teague was much appreciated.

Lastly, I would like to thank my family and friends for their unwavering support and patience during my doctoral studies. I owe more to my wife, Danielle, than she could ever imagine or I could ever repay. She has always been there for me through the countless class projects that were saved until the last minute, the innumerable hours of fieldwork, the short pay and long hours, and the countless nights of cursing at my computer. Danielle, I don't know how you've done it, but thanks for putting up with me throughout my graduate career! Dad and Barbara, Mom and Jack, and Fred and Kay, thank you for always being there and for supporting me beyond my wildest expectations -- you have all been great parents to me and I am honored to have been blessed with your love and friendship. The rest of my family members have each done their part to help me through my doctoral studies. Therefore, I thank Grandma, Granddad, Mommom, Daddad, Patrick, Jerm, Robert (you are close enough to be considered family), Donnielle, Kristi, and Kirstin for all that you have done. I owe all of my success to these people - my family.

Portions of this study and data used in this study were funded by 3 sources: the U.S. National Park Service; the Great Smoky Mountains Conservation Association's Carlos C. Campbell Memorial Fellowship; and McIntire-Stennis Project No. 55, the Agricultural Experiment Station, Department of Forestry, Wildlife, and Fisheries, The University of Tennessee, Knoxville.

ABSTRACT

To assess the impact of perceived poaching on black bears (*Ursus americanus*) within Great Smoky Mountains National Park (GSMNP), I used 31 years (1968 – 1998) of data to compare population characteristics between 2 study areas. I incorporated 1,015 captures of 705 bears into 4 models to estimate population abundance. I calculated density by delineating an effective study area as the region defined by circumscribing all trapsites with the average summer home range radius of bears in GSMNP. Mean density estimates ranged from 0.73 to 1.63 bears/km^2 on the North Carolina study area (NCSA) and from 0.65 to 1.77 bears/km^2 on the Tennessee study area (TNSA). I compared sex ratios, age structures, body sizes, litter sizes, female survival rates, and densities between the NCSA and TNSA. Density, as estimated by back dating, was the only parameter that differed, averaging approximately 25% lower on the NCSA. I determined that habitat quality driven by differences in white oak prevalence, not poaching, most likely explained the higher density of bears on the TNSA compared to the NCSA. Bait-station indices reflected the lower density of bears on the NCSA and correlated significantly with back dating estimates. Male bears traveled greater distances between captures than females and young bears delayed dispersal until 2.5 – 3.5 years of age. Although males moved long distances more frequently than females, few individuals dispersed. These movement patterns indicated that colonization of lost range would be slow and unlikely across large areas of unsuitable habitat. Weights and morphometrics of bears fluctuated

through time, but did not exhibit a clear pattern relative to fall hard mast availability. Bears seemed able to exploit soft mast and other food sources to ameliorate low hard mast production, but still were affected by overall food availability. Densities increased during years of adequate food supply to levels exceeding 1.0 bear/km^2, and then declined sharply after mast failures. During this study, such declines were followed by synchronized breeding, prolific cub production, and rapid population rebounds. Future management and research efforts should account for the impact of periodic food shortages on population ecology of bears in GSMNP.

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CHAPTER I

INTRODUCTION

Problem Statement and Justification

Black bears (*Ursus americanus*) are wide-ranging with relatively low reproductive output compared to many mammals. Densities may be as low as 0.09 bears/km^2 and females normally produce successful litters every 2 years. Because of these life history traits, and because of prior unregulated killing and habitat loss, black bear populations in the southeastern United States have been vulnerable to extirpation. Accordingly, over the past 30 years management efforts have focused on increasing bear abundance through the protection of core breeding populations, regulation of hunting, and expansion of suitable habitat. These efforts largely have been successful. From a low of small scattered populations restricted to remote terrain in the early 1900s, black bears in the Southeast now occur as many large populations that number in the hundreds or thousands. Management and protection have been so effective that in some areas bear populations are expanding back into habitats previously lost. Bears are also moving out of their historically remote landscapes and inhabiting forested tracts close to human development. Concomitant with this expansion, human populations in the Southeast also have grown. The distribution of people has shifted from a predominantly urban population at the turn of the century to a largely suburban population now. Thus, as bears have expanded from remote core areas, human development has infringed upon these same areas. Along this

suburban/wildlife interface, human-bear conflicts are inevitable. Bears are attracted by sources of high-energy food, leading to nuisance activity. Nuisance bears often are translocated or must be killed. Even if bears do not become nuisance animals, higher road densities and traffic volumes may result in greater bear mortality due to vehicle collisions.

These 2 opposing forces, increasing numbers of bears and increasing human development, present a challenge for bear managers. Whereas bear populations seem healthy and appear to be expanding, human encroachment leads to habitat fragmentation, population isolation, and increased mortality. The result is less room for management error and the need for accurate and timely information on the status, trend, and health of bear populations.

Unfortunately, such data are particularly difficult to collect for these secretive, wide ranging, and long-lived mammals. Intensive trap-recapture studies that last several years often are necessary to accumulate sufficient data to calculate population parameters like abundance, survival, and natality. Short-term studies generally cannot address the environmental fluctuations such as weather patterns, seasonal or annual food abundance, and other unknown parameters that influence population dynamics. Population responses to these sources of variation can only be studied through systematic and consistent long-term studies. One such study is the 32-year research effort on black bears in Great Smoky Mountains National Park (GSMNP, Park).

Research on black bears in GSMNP was initiated in 1968 when Dr. Michael R. Pelton and his graduate students from the University of Tennessee began a

comprehensive study. Early projects obtained baseline data and developed field and lab methodology (Johnson and Pelton 1980). These initial studies estimated the population size of bears in the Park (Lafollette 1974, Marcum 1974, Pelton and Marcum 1975, Pelton and Beeman 1975) and documented basic aspects of bear behavior (Bacon 1973, Jordan 1979), population characteristics (Beeman 1975, Pelton and Beeman 1975), nutrition (Beeman 1971, Beeman and Pelton 1977, Eagle 1979, Eagle and Pelton 1983), and denning (Johnson 1978, Johnson and Pelton 1979, Johnson and Pelton 1980*a*, Johnson and Pelton 1981). Later studies focused on the movement, activity, and habitat use of Park bears (Eubanks 1976, Garshelis 1978, Garshelis and Pelton 1978, Quigley et al. 1979, Garshelis and Pelton 1980, Garshelis and Pelton 1981, Quigley 1982, Carr 1983, Garshelis et al. 1982, Garshelis et al. 1983) and updated information on abundance (Eagar 1977, Matthews 1977) and denning ecology (Eiler 1981, Wathen 1983, Wathen et al. 1983, Wathen and Pelton 1984, Eiler et al. 1988). Nuisance bear management (Eagar and Pelton 1978, Tate 1979, Tate 1983a, Tate 1983b, Hastings et.al. 1987, Stiver 1991) and denning physiology (Pozzanghera 1990, Pozzanghera et al. 1986) were investigated in the mid to late 1980s. Recently, researchers have used modern techniques to more thoroughly examine habitat use (van Manen 1994), population dynamics (McLean 1991, McLean and Pelton 1991, McLean and Pelton 1994, Coley 1995), and nutrition (Inman 1997). Other aspects of black bear ecology that have been investigated include: visitor attitudes toward bears (Petko-Seus 1985, Petko-Seus et al. 1985, Petko-Seus and Pelton 1986), pathology and blood characteristics (Eubanks et.al. 1976, Beeman and Pelton

1978, Cook and Pelton 1978, Daugherty et al. 1979, Cook 1982, Beeman 1981), mark trees (Burst 1979, Burst and Pelton 1983), and response to trapping (Pedersen 1995).

GSMNP attracts over 9 million visits every year, more than any other national park in the United States. Thus, managers must balance the needs of the resources with those of the people enjoying them. Visitors are drawn to GSMNP for many reasons, but an important factor is its black bear population. People expect to see and learn about black bears while at GSMNP. As a featured management species within GSMNP (Herrmann and Bratton 1977), wildlife managers must be knowledgeable about the status, ecology, and demographics of GSMNP bears.

In addition to its role as a national park, GSMNP serves as a de facto sanctuary where black bears are protected from hunting and human development. However, many GSMNP bears reside outside of park boundaries partly, seasonally, or completely during some point of their life cycle. These individuals are subjected to mortality and habitat impacts while outside GSMNP and interact with full-time residents. Consequently, nuisance activities, road kills, and hunter harvest of bears outside GSMNP are affected by the dynamics of bears within GSMNP and vice versa. State and federal natural resource agencies in the region (GA, NC, SC, and TN) are interested in the demographics of bears within GSMNP to guide bear management within their respective jurisdictions. Moreover, because of perceived differences in density within the Park, as indicated from bait-station indices (Fig. 1.1) and law enforcement accounts, Park biologists suspect that illegal killing of bears may be occurring. The indistinct boundary between black bears in GSMNP and other areas in the region, coupled with the Park's large size, relative

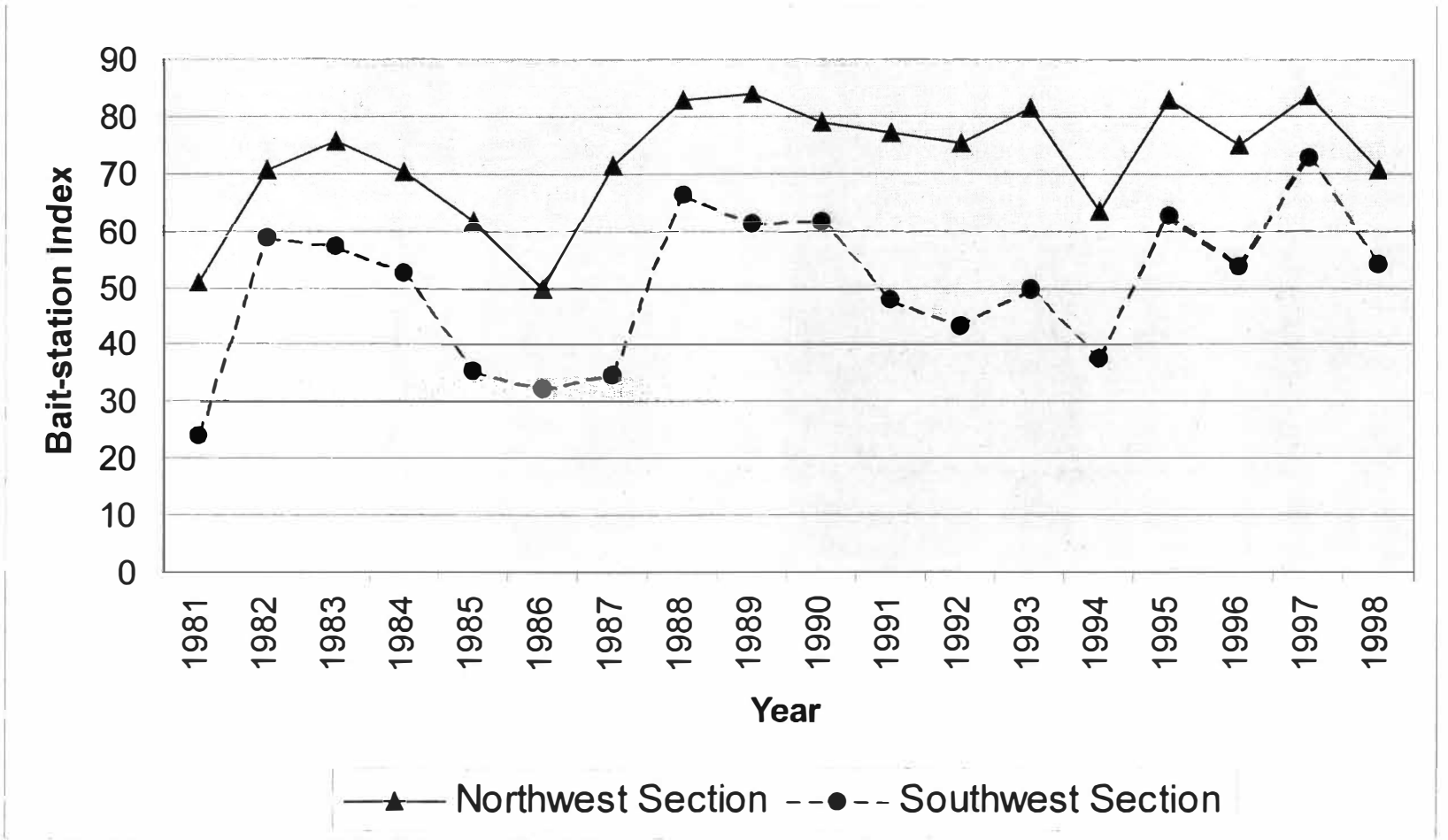


Figure 1.1. Visitation rates of black bears at bait-station sites within the northwestern and southwestern sections of Great Smoky Mountains National Park, summers 1981 - 1998.

freedom from outside influences, and extensive research base, make GSMNP an ideal area for exploring new research techniques and investigating the population ecology of the American black bear (Pelton and van Manen 1997). Therefore, the overall objective of my study was to document the population characteristics of black bears in GSMNP to ascertain if population dynamics of bears varied due to poaching or other factors.

General Study Area

The area of interest for this study was GSMNP, which lies in the southern Appalachian Mountains along the state boundary of North Carolina and Tennessee (Fig. 1.2). The Park is located between 35° 26' to 35° 47' North latitude and 83° 2' to 84° 0' West longitude and covers approximately 210,000 ha. GSMNP encompasses portions of Haywood and Swain counties in North Carolina and Blount, Cocke, and Sevier counties in Tennessee. Three national forests and an Indian reservation lie adjacent to GSMNP, and, collectively, represent a vast, contiguous block of protected lands in the region that totals approximately 1,700,000 ha of forested habitat.

Cherokee Indians originally inhabited the area that is now GSMNP. Scattered groups of these Native American peoples were engaged in a predominantly hunter-gatherer lifestyle; consequently, they had relatively low impact on the forests compared with the Europeans who later settled the area. The first Europeans came to the southern Appalachians in the 1600s mostly as fur trappers and traders. Those explorers and woodsmen laid the groundwork for settlement in small communities such as Cades Cove in Tennessee and Proctor in North Carolina. The commencement of commercial logging

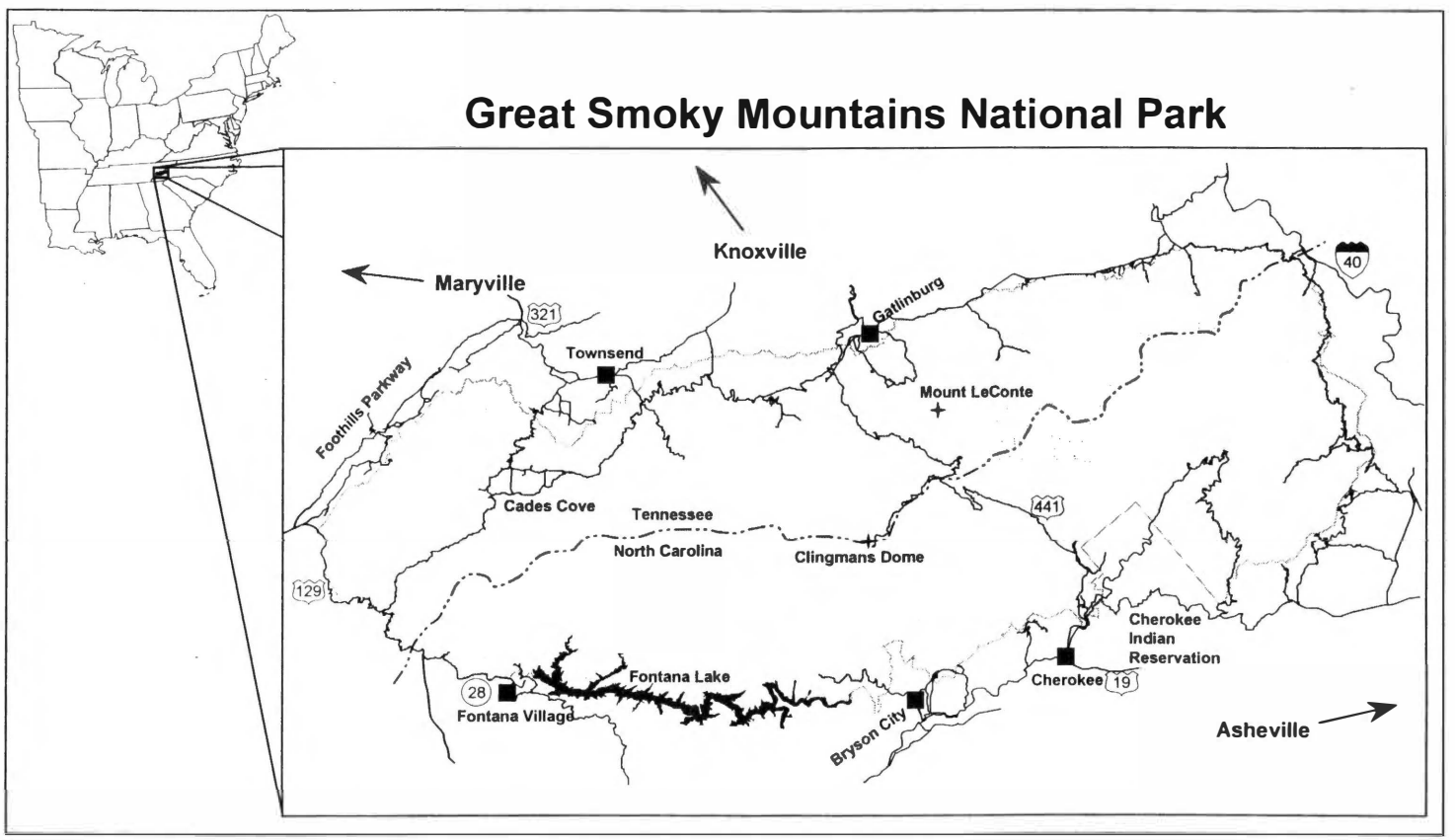


Figure 1.2. Location of Great Smoky Mountains National Park and vicinity in eastern United States.

in the late 1800s brought an influx of workers, families, and materials. Even so, the relatively isolated logging communities had minor overall impact on the forests. With the advent of large-scale cable logging in the early 1900s, timber extraction reached considerable levels. By the time GSMNP was created in 1934, > 60% of the Park area had been logged or altered by human occupation.

Impetus for the creation of GSMNP began in the early 1920s as local residents from Knoxville and other communities realized that, without protection, the natural wonders of the Smokies might be lost forever. A long and difficult campaign to create GSMNP ensued. Overcoming both regional and national political resistance, local Park Commissions garnered support for the Park and raised monies to purchase lands. Inflationary land prices associated with the Great Depression almost undid plans for GSMNP; however, a large donation from the Rockefeller family followed by federal monies enabled completion of land purchases. Congress finally established GSMNP on 15 June, 1934 and President Franklin D. Roosevelt officially dedicated the Park on 2 September, 1940. More recently, GSMNP was named an International Biosphere Reserve in 1976 and a World Heritage Site in 1983.

Since its inception, GSMNP has served as a haven for people who wish to experience nature and wildlife. Most visitors come to view the spectacular vistas and natural scenery along the twisting and winding roads that traverse the Park. Many also come to experience the outdoors and enjoy the recreational opportunities provided by GSMNP. Hiking, camping, wildlife and wildflower viewing, kayaking, horseback riding, biking, and tubing, among countless other activities, are visitor favorites. Because of its

high human use rate, interactions between people and wildlife such as bears are common in the Park.

Great Smoky Mountains National Park lies in the Southern Appalachian Highlands which is part of the Unaka Mountain Range of the Blue Ridge Province (Fenneman 1938). The primary ridge crest extends northeast to southwest and forms the state boundary between North Carolina to the east and Tennessee to the west. Topography is characterized by distinct ridges and steep, stream-cut valleys (King and Stupka 1950). Present day ridges, with their extensive weathering and blunted features, are the artifact of countless millennia of erosion upon a once great, upland plateau. Current elevation ranges from 266.4 m at Chilhowee Lake to 2,024.8 m at Clingman's Dome. Slopes tend to be moderate to steep and exceed 10% throughout 90% of the Park (King and Stupka 1950). Sandstone rock formations of the Ocoee Series from the Precambrian Era dominate the geology of the area (King et al. 1968). Soils are of the Ramsey Association, with Ramsey Series occurring on mountain slopes and Jefferson Series occurring on lower slopes. These soils are characterized by low water storage, medium to high acidity, and moderate fertility (Soil Survey 1945, 1953, Golden 1974).

Thornthwaite (1948) characterized the climate of GSMNP as a warm, temperate rainforest. However, the combinations of elevation, aspect, slope, and topographic features contained within GSMNP result in tremendous variation in microclimates (Shanks 1954a). Mean annual temperatures vary from 14°C at elevations < 450 m to 8°C at elevations > 1,900 m (Stephens 1969). Mean monthly temperature ranges from 4.4°C to 22°C and from –1.8°C to 13.5°C at these same elevations, respectively; lowest

temperatures are reached in February, whereas highest temperatures are reached in July. Generally, a 1,000-m rise in elevation results in a 4°C decline in temperature, or, the equivalent of moving approximately 1,300 km northward. Precipitation amounts vary from 140 cm per year at lower elevations to > 220 cm per year at higher elevations (Stephens 1969). July is the wettest month, whereas September and October are the driest months (Dickson 1960, Stephens 1969). Shanks (1954*a*) reported snowfall on 6.75 days per year at lower elevations and 25.9 days per year at higher elevations; mean annual snowfall was approximately 63 cm.

These differences in microclimates have resulted in great richness of plant life within GSMNP. Whittaker (1956) described the Park as having the greatest diversity of flora in all of the eastern forests. More than 1,300 species of flowering plants, including > 130 species of trees, inhabit GSMNP (Stupka 1960). Moreover, > 2,000 species of fungi, 330 species of mosses, 230 species of lichens, and 32 species of ferns occur park-wide (King and Stupka 1950). The vegetation of GSMNP has been studied by many researchers, but most notably by Shanks (1954*b*) and Whittaker (1956). More recently, MacKenzie (1991, 1993) used remote sensing data and geographic information system analyses to create an updated overstory vegetation classification for the Park. MacKenzie's classification system identified 9 forest cover types that are distributed throughout GSMNP (Table 1.1). Within this system, cove hardwood, mixed mesic hardwood, and pine were the most common cover types. Common understory species included mountain laurel (*Kalmia latifolia*), rhododendron *(Rhododendron spp.*), huckleberry (*Gaylussacia* spp.), and greenbriar (*Smilax* spp.).

Table 1.1. Scientific and common names of dominant forest types in Great Smoky Mountains National Park (adapted from MacKenzie 1991, 1993).

Forest Type	Dominant Tree Species[1]	
	Scientific Name	Common Name
Spruce – Fir	*Betula lutea*	Yellow Birch
	Picea rubens	Red Spruce
	Acer rubrum	Red Maple
Northern Hardwood	*Betula lutea*	Yellow Birch
	Fagus grandifolia	American Beech
	Betula lenta	Sweet Birch
	Tsuga canadensis	Eastern Hemlock
	Acer rubrum	Red Maple
	Quercus rubra	Northern Red Oak
	Picea rubens	Red Spruce
Cove Hardwood	*Tsuga canadensis*	Eastern Hemlock
	Betula lenta	Sweet Birch
	Acer rubrum	Red Maple
	Halesia carolina	Carolina Silverbell
	Liriodendron tulipifera	Tulip Poplar
	Quercus rubra	Northern Red Oak
	Tilia heterophylla	American basswood
	Betula lutea	Yellow Birch
Mesic Oak	*Quercus rubra*	Northern Red Oak
	Acer rubrum	Red Maple
	Quercus prinus	Chestnut Oak
Mixed Mesic Hardwood	*Liriodendron tulipifera*	Tulip Poplar
	Acer rubrum	Red Maple
	Tsuga canadensis	Eastern Hemlock
	Quercus prinus	Chestnut Oak
Tulip Poplar	*Liriodendron tulipifer*	Tulip Poplar
	Acer rubrum	Red Maple
	Halesia carolina	Carolina Silverbell

Table 1.1. (Cont.)

Forest Type	Dominant Tree Species	
	Scientific Name	Common Name
Xeric Oak	*Quercus prinus*	Chestnut Oak
	Acer rubrum	Red Maple
	Liriodendron tulipifera	Tulip poplar
	Oxydendrum arboreum	Sourwood
	Quercus coccinea	Scarlet Oak
Pine – Oak	*Quercus coccinea*	Scarlet Oak
	Pinus pungens	Table Mountain Pine
	Nyssa sylvatica	Black Gum
	Acer rubrum	Red Maple
	Quercus prinus	Chestnut Oak
Pine	*Pinus pungens*	Table Mountain Pine
	Pinus rigida	Pitch Pine
	Pinus virginiana	Virginia Pine
	Quercus coccinea	Scarlet Oak

[1]Species with mean basal area > 2.0 m^2/ha ordered within forest types by dominance (from MacKenzie 1991, 1993).

GSMNP is home to a wide diversity of animals. Linzey and Linzey (1971) documented 59 species of mammals, approximately half of which were rodents. Six species of mammals have been extirpated from the Park in the recent past. Management efforts to reintroduce 3 of these species have met with mixed results. The river otter (*Lutra canadensis*) seems to have been successfully reintroduced in the mid 1990s, but similar attempts for the red wolf (*Canis rufus*) met with failure. Feasibility of reintroducing elk (*Cervus elaphus*) has been studied with positive results and release efforts are in the preliminary phases. Other than humans, the 3 large mammals found in GSMNP are the black bear, white-tailed deer (*Odocoileus virginianus*), and wild hog (*Sus scrofa*). Other fauna include > 200 species of birds (of which > 110 species breed in the Park), > 130 species of reptiles, 39 species of amphibians, and 70 species of fishes (King and Stupka 1950).

CHAPTER II

ESTIMATION OF POPULATION SIZE

Introduction

The most accurate method of estimating the size of wildlife populations is to perform a total count of all individuals. This technique is achievable for highly visible species residing in open areas, but is untenable for most wildlife species, which exhibit cryptic morphology and behaviors. For these species, researchers have relied on methods that enable estimation of population size by statistical sampling. Techniques have included removal studies that approximate total counts, point and line transect techniques that sample known areas, and mark-recapture procedures that compare ratios of marked and unmarked individuals sampled at different times (Caughley 1977, Krebs 1998). Because of the low densities and secretive habits of most large carnivores, estimates of population size have primarily been based on mark-recapture methodology. Considerable technical progress has been made whereby a wide array of models with varying assumptions are available to wildlife biologists (Caughley 1977, Seber 1982, Krebs 1998).

In GSMNP, black bear research has advanced from basic demographic studies to implementation of advanced mark-recapture methodology to estimate population size. Early studies described the Park's history of preserving the last enclaves of bears in east Tennessee in the early 1900s (Lafollette 1974) and documented its role as a de facto

sanctuary (because hunting is not allowed) (Beeman 1975). Before bear research was initiated in GSMNP, the National Park Service estimated that approximately 50 – 300 bears inhabited the Park. Beeman (1975) first described the basic aspects of black bear population characteristics in the Park in the early 1970s. His work focused on developing methods to study free-ranging black bears and applying them to determine basic population parameters. Based on this research, Beeman (1975) revised the National Park Service's estimate of 50-300 bears in GSMNP to 300+ bears, a minimum average density of 0.14 bears/km^2.

Following Beeman's work on population characteristics, research focused on predicting abundance and density of bears in the Park. Marcum (1974) conducted a radioisotope tagging study in which captured bears were administered a dosage of radioactive zinc (^{65}Zn) or manganese (^{54}Mn). Scats were subsequently collected along trails within the study area and the ratio of radioactive to normal scats was used to generate a population estimate. Using this method, Marcum (1974) estimated that the density of bears within the study area was 0.36 bears/km^2. Eagar (1977) continued the radioisotope tagging effort and estimated bear densities within the study area at 0.33 and 0.36 bears/km^2 for 1974 and 1975, respectively. However, due to an assumed higher quality of bear habitat in the study area as compared to other areas of GSMNP, these researchers hypothesized that the average density of bears in GSMNP was lower than that estimated by their work. Thus, estimates for the number of black bears in GSMNP at that time were revised to 300 – 500 bears.

Building on the work of Marcum and Eagar, Matthews (1977) attempted to devise an index to bear density by recording the number of scats encountered along trails in GSMNP. She found that variability in scat occurrence because of weather, bear behavior, and topographic location prohibited the development of an accurate index. A bait-station survey was developed in the early 1970s and initiated in the late 1970s to track trends in bear density. An index derived from the bait-station survey was based on the percentage of baits taken by bears. A preliminary examination by Johnson and Pelton (1983) found that this percentage correlated with population estimates for the northwest portion of GSMNP. Following this work, bait-station routes were established throughout GSMNP and have since been conducted each year in the summer. If more detailed analyses covering larger areas demonstrate that bait-station surveys correspond to population abundance, they could be used to monitor bear densities over large areas where more rigorous and labor-intensive trapping is not feasible.

During the late 1970s to mid 1980s, the focus of bear research in GSMNP shifted from population characteristics to activity, movements, home-range delineation, and denning ecology. Throughout this period, bait routes and other observations suggested that the bear population continued to increase, prompting research once again to turn toward population estimation and dynamics. McLean (1991) employed traditional trap-recapture data with a newly developed model, the Jolly-Seber open population model, and found that the bear population in the late 1980s was increasing at 2-5% annually. Additionally, he concluded that the average density of bears in the study area was 0.33 bears/km^2 (McLean 1991, McLean and Pelton 1994). Coley (1995) used GSMNP data

collected from 1973 - 1991 (887 bear captures) and used a revised study area size based on the distance of activity centers from capture sites. Based on this method, the estimated density of black bears in the study area was revised to an average of 1.56 bears/km^2, a much higher density than that found by McLean.

Coley's (1995) study raised several questions regarding the accuracy of the estimates, violation of model assumptions, and study area delineation. Was it possible that GSMNP harbored one of the densest bear populations documented (Garshelis 1994), or were Coley's (1995) estimates biased by undetermined factors? How had the use of an effective study area affected the results compared to earlier studies' traditional study area delineation? Was the density of bears uniform throughout the Park, or were bears less dense in sections of GSMNP other than the study area? Have other data like bait-station surveys within the Park mirrored the increase in bear numbers found by Coley? These questions were unanswerable with data available from the traditional study area and required the use of new techniques and study areas. Thus, the objective of my study was to utilize new techniques and methodology to determine black bear population size in Great Smoky Mountains National Park. Specific objectives were to:

1. estimate the number of black bears in the south- and northwestern quadrants of GSMNP;
2. investigate the use of remote camera stations as a resight technique for estimating black bear population size;
3. determine a biologically meaningful radius of effective sampling around bear trapsites; and

4. determine if bait-station visitation correlated with population estimates of black bears.

Study Area

I defined 2 study areas within GSMNP by buffering trapsites on each side of the Park with an estimated radius of use (see Methods) and taking the cumulative area of these buffers (Fig. 2.1). Although this procedure resulted in 2 pairs of areas on each side of the Park, I combined each pair to bolster analyses by increasing sample sizes and sampling areas. The North Carolina study area (NCSA) was established for this study in summer 1994 and was active for 5 years, through summer 1998. This study area totaled 400 km^2 and consisted of 8 traplines that stretched eastward from the southwestern boundary of GSMNP to highway 441 and southward from the North Carolina-Tennessee border to Fontana Lake (Fig. 2.1). This portion of GSMNP was remote and had no road system; consequently, the only means of access was via boat on Fontana Lake or hiking on backcountry trails. Because of these factors, visitor use of the area was low compared with other, more easily accessible, areas of GSMNP. The Tennessee study area (TNSA) was established in 1989 and was sampled continuously through 1998. This TNSA totaled 358 km^2 and consisted of 8 traplines that stretched eastward from the northwestern boundary of GSMNP to highway 441 and northward from the North Carolina-Tennessee border to the northern boundary of the Park (Fig. 2.1). Several paved roads traversed this portion of GSMNP and provided access to popular areas such as Cades Cove, Tremont, and Sugarlands; consequently, visitor use rates were high.

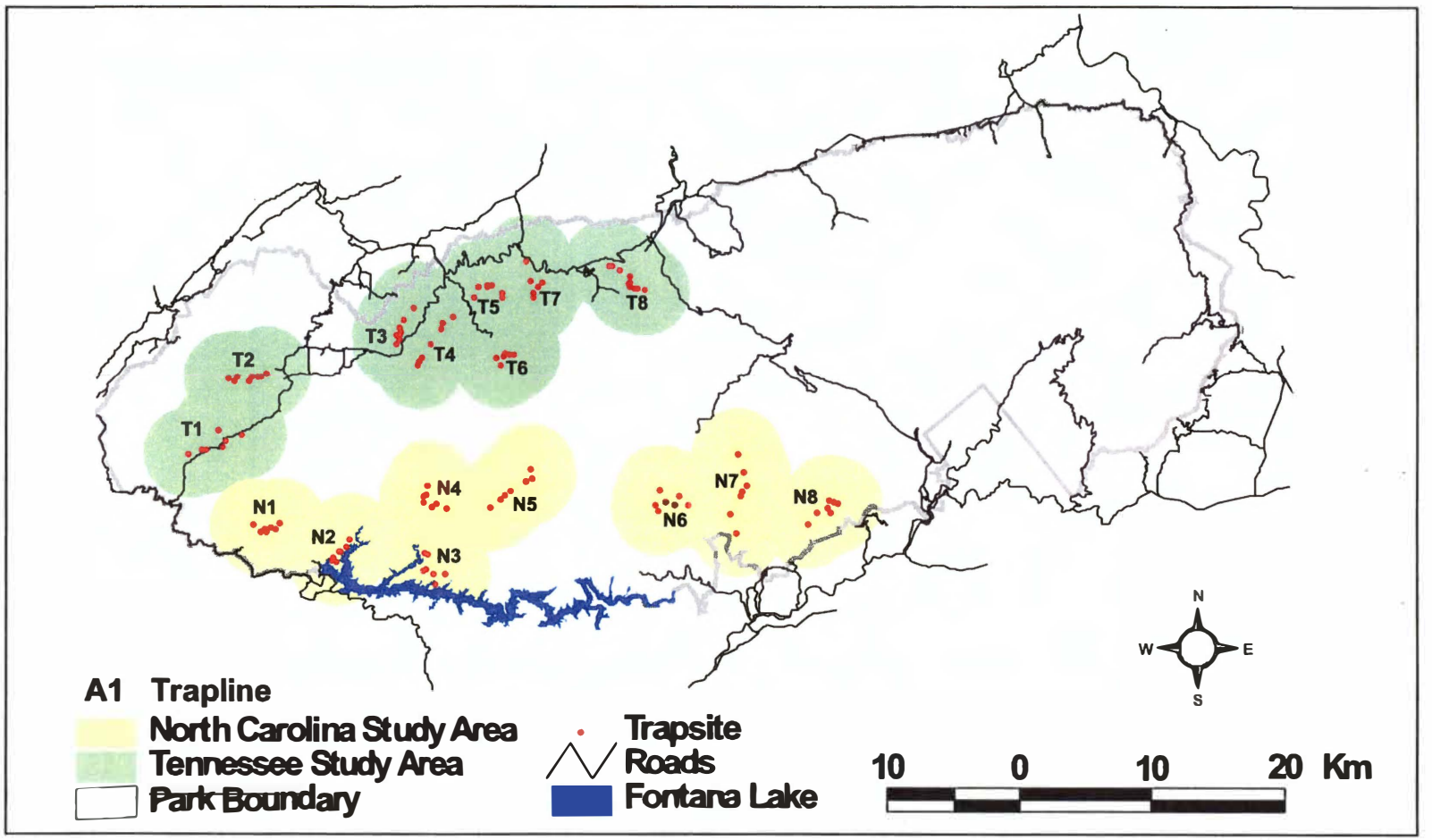


Figure 2.1. Location of traplines and trapsites within North Carolina and Tennessee study areas in Great Smoky Mountains National Park, 1989 – 1998. See Table 2.2 for meaning of trapline codes.

Methods

I integrated data previously collected on bears in GSMNP from 1989 to 1993 with current data collected for this study from 1994 to 1998. I used an existing database that was compiled from former studies conducted in the TNSA and appended it with new data that was collected on bears within the NCSA and TNSA from 1994 to 1998.

Trapping. Data were collected from 705 individual black bears captured a total of 1,015 times from both study areas (Table 2.1). Personnel compiled 295 captures of 224 individual bears in the NCSA from 1994 to 1998 and 720 captures of 481 individual bears in the TNSA from 1989 to 1998. I coordinated the capture of black bears in the NCSA and TNSA from 1994 to 1997 and personally led trapping efforts on the NCSA during this time period. Other personnel from the University of Tennessee collected preceding data in the TNSA from 1989 to 1993 and subsequent data from both study areas in 1998. The TNSA consisted of 8 traplines with 6 – 9 trap sites each; traplines averaged 587 m between successive trapsites, and trapsites averaged 774 m in elevation (Table 2.2). The NCSA consisted of 8 traplines with 7 trapsites each; trapsites averaged 908 m in altitude and 694 m between them (on each line) (Table 2.2). Establishment of traplines and trapsites in the NCSA took several days in 1994 and resulted in less trapping effort that year compared with subsequent years (Table 2.1). The NCSA traplines were placed to approximate the elevations and topographic positions of the TNSA traplines. All trapsites were positioned away from trails so that hikers could not easily see or hear captured bears.

Table 2.1. Trapping data from North Carolina and Tennessee black bear study areas in Great Smoky Mountains National Park, summers 1989 - 1998.

Year	Study Area[1]	Trapnights	Total Captures	Initial Captures	Within Year Recaptures	Previous Year Recaptures	Trapnights per Capture
1989	TNSA	697	78	75	3	0	8.9
1990	TNSA	560	41	34	0	7	13.7
1991	TNSA	737	52	40	1	11	14.2
1992	TNSA	762	52	37	3	12	14.7
1993	TNSA	806	27	16	1	10	29.9
1994	TNSA	783	66	45	3	18	11.9
	NCSA	431	27	27	0	0	16.0
1995	TNSA	784	98	60	8	30	8.0
	NCSA	780	60	52	5	3	13.0
1996	TNSA	791	82	50	5	27	9.6
	NCSA	777	63	49	6	8	12.3
1997	TNSA	793	135	72	16	47	5.9
	NCSA	776	89	59	6	24	8.7
1998	TNSA	780	89	52	9	28	8.8
	NCSA	732	56	37	2	17	13.1
Total	TNSA	7,493	720	481	49	190	10.4
	NCSA	3,496	295	224	19	52	11.9
Grand Total	Both	10,989	1,015	705	68	242	10.8

[1]TNSA = Tennessee study area; NCSA = North Carolina study area.

Table 2.2. Trapline characteristics for North Carolina and Tennessee black bear study areas in Great Smoky Mountains National Park, summers 1989 - 1998.

Code	Trapline	# Trapsites	Order Trapped	Average Distance Between Trapsites (m)	Average Altitude of Trapsites (m)
	North Carolina Study Area:				
N1	Twentymile Loop	7	1	454	734
N2	Lakeshore Dam	7	1	456	604
N3	Lakeshore West	7	4	719	641
N4	Jenkin's Ridge	7	2	579	914
N5	Hazel Creek	7	2	748	856
N6	Springhouse Branch	7	4	844	1,150
N7	Noland Divide	7	3	1,078	1,339
N8	Deeplow Gap	7	3	673	1,023
---	Average	7	---	694	908
	Tennessee Study Area:				
T1	Parson's Branch	7	2	989	831
T2	Rabbit Creek	7	2	483	655
T3	Turkey Pen Ridge	6	3	333	600
T4	Bote Mountain	7	3	768	769
T5	Lumber Ridge	7	1	530	719
T6	Green Camp Gap	7	1	405	917
T7	Curry Mountain	6	4	724	788
T8	Sugarland Mountain	9	4	415	910
---	Average	7	---	581	774
---	Overall Average	7	---	638	841

Project personnel captured and handled bears by means of standard techniques (Johnson and Pelton 1980) every summer from May to August. Two crews on each study area trapped 2 traplines simultaneously for 15 days each. Then, after a 2 – 4 day hiatus, crews moved to the next 2 traplines. This process resulted in 4 trapping periods each summer on each study area (Table 2.2). Although cubby sets predominated, trail sets, brush cubbies, trick sets, and double sets were also used.

Personnel immobilized bears by injecting a mixture of Ketaset (ketamine hydrochloride, Aveco Co., Inc., Fort Dodge IA), Rompun (xylazine hydrochloride, Rugby Laboratories, Inc., Rockville Center, NY), and Carbocaine-V (mepivicaine hydrochloride, Sterling Drug Inc., McPherson, KS) (KRC) at a ratio of 200 mg Ketaset: 100 mg Rompun: 20 mg Carbocaine. Personnel administered KRC intramuscularly via jab pole syringe or blowpipe dart at 1 cc per 25 kg. Once immobilized, bears were treated with ophthalmic ointment to moisturize eyes and triple anitbiotic to disinfect minor cuts and wounds. Personnel subsequently measured, weighed, ear-tagged, and lip-tattoed all bears. Also, a premolar tooth was extracted for aging by counting cementum annuli (Willey 1974). Selected adult females and yearlings were fitted with radio collars (Telonics, Mesa, Ariz. and Ursus Technologies, Williamsburg, Virginia). In 1996, personnel placed colored ear streamers and 2-inch wide cotton collars on bears in both study areas for identification at remote camera stations. Orange streamers and collars were used on the Tennessee study area whereas yellow streamers and collars were used on the North Carolina study area. In 1997 and 1998, personnel placed green or blue and orange colored ear streamers, respectively (without collars) on bears in the North

Carolina study area only. Personnel revived bears with intavenous injections of Yohimbine (Lloyd Laboratories, Shenandoah, IO) and recorded all data on standard University of Tennessee bear capture forms.

Remote Cameras. I coordinated the collection of remote camera resight data from 1996 to 1998. In 1996, remote camera stations were placed along traplines immediately after trapping ceased in both study areas. Personnel collected resight data from the initial 2 traplines while trapping crews trapped the next 2 traplines. Thus, remote camera sampling started 15 days after the initiation of trapping and continued for 15 days after the completion of trapping. Personnel checked and reset camera stations every other day and sampled each trapline for 15 days. In 1997 and 1998, I collected resight data after the completion of all trapping in the North Carolina study area (remote camera stations were not used on the Tennessee study area). I placed remote camera stations on 3 – 5 traplines at a time, moving cameras to new traplines as I finished earlier ones. I checked and reset camera stations every 4 – 5 days and sampled each trapline for 15 – 30 days. All camera stations were placed at about 1-km intervals along the traplines, but were offset from trapsites as far as possible. By doing so, I hoped to avoid any residual bias from bears accustomed to bait or capture at the trapsites.

The remote camera stations consisted of an inexpensive single-shot camera mounted into a wooden box (1996) or ammunition can (1997 and 1998) for protection (Martorello et al. 2001). A nylon string attached to the bait activated the shutter mechanism of the camera. The camera box was nailed to a tree that faced another tree

approximately 2 m away (Figure 2.2). Thus, when a bear tugged on the bait, the camera was activated and a picture of its head and shoulders was taken (Figure 2.3).

I tested the potential for camera station placement to induce trap response from bears through a field test. After trapping in summer 1997, I intensively sampled a small study area consisting of 2 traplines (Springhouse Branch and Deeplow Gap) with remote cameras. I sampled this area twice, once with camera stations placed adjacent to existing trapsites and once with them offset from trapsites. Thus, I was able to test for trapsite response in the camera sampling effort. To accomplish this objective, I used Fisher's Exact Test (SAS Inst. Inc. 1990) on the distribution of resights of bears at the 2 camera locations at the $\alpha = 0.05$ level. I tested the following null and research hypotheses:

H_0: Frequency of marked and unmarked bears did not differ between cameras placed at trapsites and those placed away from trapsites.

H_R: Frequency of marked bears was greater, and unmarked bears less, for cameras placed at trapsites than for those placed away from trapsites.

Abundance. Most methods of estimating animal abundance are based on marking a portion of a population followed by resampling to determine the size of the marked portion. Models for population estimation have become increasingly complex. The earliest models (e.g. Lincoln-Petersen) used a ratio of marked to unmarked animals from 2 samples. These models required restrictive assumptions regarding population closure that are difficult to achieve with large, wide-ranging animals like black bears.

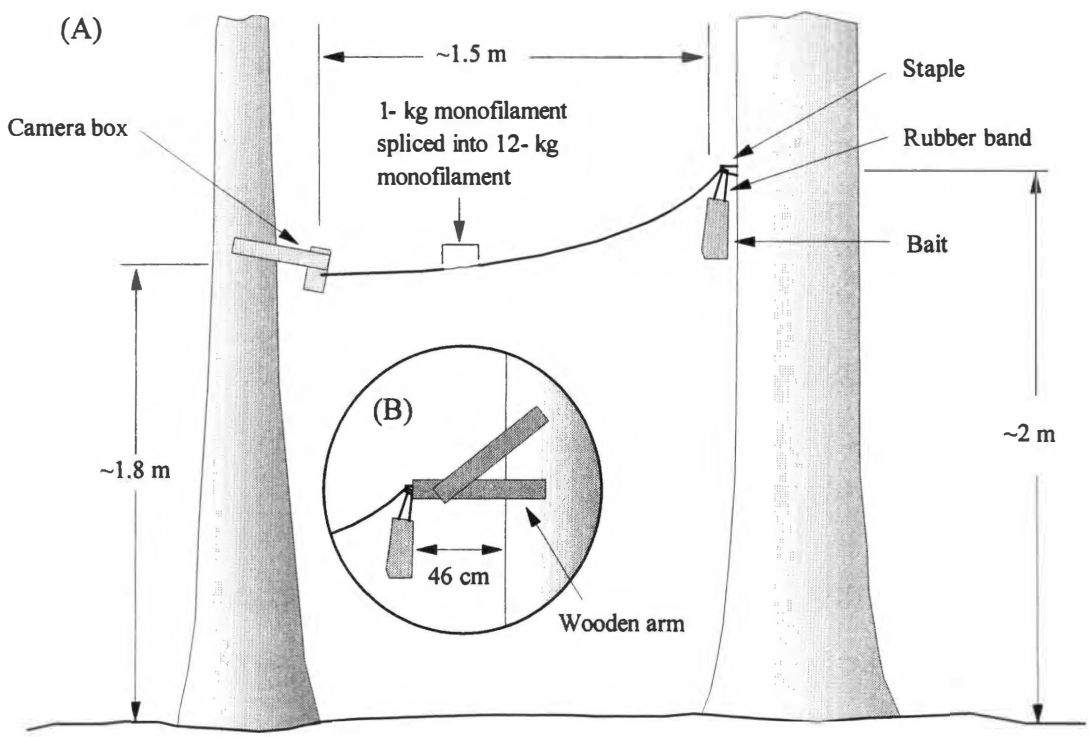


Figure 2.2. Remote camera station setup (A) without and (B) with small mammal deterrent option for resight study of black bears in Great Smoky Mountains National Park, summers 1996 – 1998 (from Martorello et al. 2001).

(A)

(B)

Figure 2.3. Sample photographs of (A) unmarked and (B) marked bears from remote camera resight study of black bears in Great Smoky Mountains National Park, summers 1996 – 1998.

Subsequent models (e.g. Jolly-Seber) allow for relaxation of this assumption, but required multiple sampling periods and often lack sufficient precision when applied to large mammals like bears that are difficult to catch. Because of the limitations with all models, Pollock et al. (1990) recommended a combination of models to achieve optimal precision and accuracy.

I generated abundance estimates using 4 methods: Lincoln-Petersen, Bailey's binomial, and back-dating models for closed populations, and the Jolly-Seber model for open populations. Data from the remote camera resight study were used in the Bailey's binomial model, whereas data from the summer trapping seasons were used in the 3 other models.

The Lincoln-Petersen model was developed as an estimator of population size for demographically closed populations, i.e., populations with no emigration, immigration, mortalities, or natalities. This model estimates population size by the simple ratio of marked to unmarked individuals from 2 samples. To correct for bias associated with the original model, Chapman (1951) modified the equation to its currently used form:

$$N = \frac{(M+1)(n+1)}{(m+1)} - 1$$

where: N = population estimate,

M = number of individuals marked during the first sample,

n = total number of individuals captured in the second sample,

m = number of marked individuals in second sample.

Seber (1970, 1982) derived an approximately unbiased estimate of variance of the modified Lincoln-Petersen equation as:

$$\sigma_N^2 = \frac{(M+1)(n+1)(M-m)(n-m)}{(m+1)^2(m+2)}$$

where σ_N^2 = the estimated variance of the population estimate and the other parameters are as in the above equation.

The explicit assumptions of the modified Lincoln-Petersen model are: 1) equal catchability of all individuals, 2) marks are not lost or overlooked, 3) no mortality or emigration occurs between samples, and 4) no natality or immigration occurs between samples. Assumptions 3 and 4 may be relaxed if deletions (mortality and emigration) are roughly equal to additions (natality and immigration) or if deletions occur randomly with respect to marked and unmarked individuals (Pollock et al. 1990). In these cases, the estimate will be valid for the second sampling period. Although sampling bears over a large time interval (1 year) violated these assumptions, I used the modified Lincoln-Petersen model as a baseline for comparison with the other estimators. Also, to avoid further sampling problems, I deleted within-year recaptures and cubs from the analysis; therefore, the estimates were for bears of yearling age or older. I incorporated capture data from 1989 to 1998 on the TNSA and from 1994 to 1998 on the NCSA into the Lincoln-Petersen model (Table 2.3). Because the sampling distributions for the Lincoln-Petersen estimates were asymmetrical (bounded below by the number of different individuals caught and unbounded above), I calculated confidence limits based on a Poisson mean (Krebs 1998).

Table 2.3. Black bear trapping data incorporated into the Lincoln-Petersen model used for North Carolina and Tennessee study areas in Great Smoky Mountains National Park, summers 1989 - 1998.

Year	Study Area[1]	# in First Sample	# in Second Sample	# Marked in Second Sample	# Cubs in Second Sample
1989 - 1990	TNSA	72	40	7	0
1990 - 1991	TNSA	40	51	3	0
1991 - 1992	TNSA	51	47	7	2
1992 - 1993	TNSA	47	26	1	0
1993 - 1994	TNSA	26	63	4	0
1994 - 1995	TNSA	63	88	17	2
	NCSA	27	53	3	0
1995 - 1996	TNSA	88	76	14	0
	NCSA	53	57	5	0
1996 - 1997	TNSA	76	115	17	1
	NCSA	57	82	9	0
1997 - 1998	TNSA	115	80	17	0
	NCSA	82	54	10	0

[1]TNSA = Tennessee study area; NCSA = North Carolina study area.

Bailey's binomial model (Seber 1982) also is used for demographically closed populations, but was developed specifically for resampling with replacement. To correct for replacement (i.e., multiple resights of the same individual), Bailey's model assumes a binomial distribution of resights and calculates its estimates accordingly:

$$N = \frac{M(n+1)}{m+1}$$

The approximate unbiased estimate of variance for Bailey's binomial equation is calculated as follows:

$$\sigma_N^2 = \frac{M^2(n+1)(n-m)}{(m+1)^2(m+2)}$$

where the variables are the same as those described for the Lincoln-Petersen model.

The assumptions of Bailey's binomial model are the same as those listed for the Lincoln-Petersen equation above. However, unlike the trapping data, the camera resight data minimized violations of these assumptions because of the narrow time interval between samples; the longest time between marking and resighting was 3 months instead of 1 year for the trapping data. Thus, bears had less time to move in or out of the study areas and mortality should have been negligible. Photographs of cubs were excluded from the model. I incorporated capture data followed by resight data from remote cameras taken during summer 1996 on the TNSA and during summers 1996 to 1998 on the NCSA into Bailey's model (Table 2.4). I calculated asymmetrical confidence limits based on the binomial distribution (Seber 1982) for the camera resight estimates.

Backdating, the final closed model to be used, assumes that all captured bears have resided in the study area since their birth. Consequently, the model simply back-

Table 2.4. Black bear remote camera data incorporated into Bailey's Binomial model for North Carolina and Tennessee study areas in Great Smoky Mountains National Park, summers 1996 - 1998.

Year	Study Area[1]	Camera Nights	Sighting Opportunities	Bear Photos: Total / Usable	Non-Target Animal Photos	Camera Nights per Usable Bear Photo	Sighting Opportunities per Usable Bear Photo
1996	TNSA	758	374	86 / 77	9	9.8	4.6
	NCSA	786	352	75 / 65	6	12.1	5.4
1997	---	---	---	---	---	---	---
	NCSA	1,034	166	122 / 108	16	9.6	1.5
1998	---	---	---	---	---	---	---
	NCSA	768	119	85 / 80	1	9.6	1.5
Total	TNSA	758	374	86 / 77	9	9.8	5.4
	NCSA	2,588	637	282 / 253	23	10.2	2.5
Grand Total	Both	3,346	1,011	368 / 330	32	10.1	3.1

[1]TNSA = Tennessee study area; NCSA = North Carolina study area.

calculates all of the known bears in each study area to the year of their birth and sums them to get a total for each year. Estimates from this model are conservative because it neglects all of the unmarked bears in the population. I used this model to give a minimum number of bears known to be alive in each study area. I incorporated capture data from 1989 to 1998 on the TNSA and from 1994 to 1998 on the NCSA into the backdating model (Table 2.1). Because of the limited data available for later years in this analysis, I used a simple linear regression to estimate abundances for the final 3 years (1996 – 1998) on each study area. For estimates that were generated from at least 3 years of data (1989 – 1995), I regressed the number captured in the first year only against the total number of bears estimated by the backdating model. The regression was highly significant and accounted for over 90% of the variation in the data (Appendix A).

I used the Jolly-Seber model as an open population size estimator for the 2 study areas (Pollock et.al. 1990). This model uses 3 or more consecutive samples to estimate population sizes for all but the first and last sampling periods. The third sample is needed for the model to estimate the survival rates, recruitment, and capture probabilities to calculate population estimates for the earlier periods. Assumptions of the Jolly-Seber model include: 1) equal probability of capture for individuals, 2) equal probability of survival for individuals, 3) samples are instantaneous, and 4) marks are not lost or overlooked. I used the computer program JOLLY (Pollock et.al. 1990) for the analyses and I input data in the capture history format. Program JOLLY uses a suite of models and tests for the one that best fits the data. These models are: Model A) survival and capture probabilities vary over sampling periods, Model A') death but no immigration, Model B)

constant survival rates, Model D) constant survival rates and capture probabilities, and Model 2) different survival rates for first time captures than for other individuals (Pollock et al. 1990). When > 1 model fit the data, I chose the one that best conformed to my understanding of the trapping dynamics within the data. I incorporated capture data from 1989 to 1998 on the TNSA and from 1994 to 1998 on the NCSA into the Jolly-Seber model (Table 2.5). Because of small sample sizes and the asymmetrical nature of the sampling distribution, I followed the recommendation of Krebs (1998) and used Manly's (1984) method of calculating confidence limits.

Effective Study Area. Although the calculation of density from abundance is mathematically trivial, problems arise because of the difficulty in delineating an effective study area size (one that accurately represents the area used by the individuals sampled for the population estimate). Historically, researchers have used arbitrary boundaries such as political jurisdictions, highways, rivers, and other topographic features that may have little biological meaning to the species being studied. Small mammal researchers have employed various methods to identify the effective area of sampling during mark-recapture within a defined grid system of traps (Dice 1938, 1941, Mohr and Stumpf 1966, Pelikan 1967, 1968, 1971, Stickel 1954). One of these methods involved buffering trapsites by the average home range radius of the population being sampled to approximate the effective sampling area (Caughley 1977, Dice 1938, 1941). Although this buffering seems to work well for populations that are intensively sampled with closely spaced trapping grids, little work has been done to determine its application to wide-ranging animals that are sampled more extensively with fewer trap sites.

Table 2.5. Black bear trapping data incorporated into the Jolly-Seber model used for North Carolina and Tennessee study areas in Great Smoky Mountains National Park, summers 1989 - 1998.

Year	Study Area[1]	Time of Recapture										Caught	Released	Marked	Unmarked
		1989	1990	1991	1992	1993	1994	1995	1996	1997	1998				
1989	TNSA	0	7	8	3	1	1	2	0	2	1	75	72	0	75
1990	TNSA	0	0	3	2	1	1	2	1	0	0	41	40	7	34
1991	TNSA	0	0	0	7	7	3	1	0	0	0	51	51	11	40
1992	TNSA	0	0	0	0	1	9	3	1	3	0	49	49	12	37
1993	TNSA	0	0	0	0	0	4	5	2	2	0	26	26	10	16
1994	TNSA	0	0	0	0	0	0	17	9	4	2	63	63	18	45
	NCSA	—	—	—	—	—	0	3	3	4	3	27	27	0	27
1995	TNSA	0	0	0	0	0	0	0	14	19	3	90	90	30	60
	NCSA	—	—	—	—	—	0	0	5	7	0	55	53	3	52
1996	TNSA	0	0	0	0	0	0	0	0	17	5	77	76	27	50
	NCSA	—	—	—	—	—	0	0	0	9	4	57	57	8	49
1997	TNSA	0	0	0	0	0	0	0	0	0	17	119	116	47	72
	NCSA	—	—	—	—	—	0	0	0	0	10	83	82	24	59
1998	TNSA	0	0	0	0	0	0	0	0	0	0	80	80	28	52
	NCSA	—	—	—	—	—	0	0	0	0	0	54	54	17	37

[1]TNSA = Tennessee study area; NCSA = North Carolina study area.

I examined several data sets to explore possible buffer radii with which to circumscribe trapsites. In these analyses, I attempted to enumerate distances that bears traveled from known sites (usually capture sites). The first data set that I examined was from telemetry studies previously conducted in GSMNP from 1976 to 1982 and summarized by van Manen (1994). I used these data in 2 ways. In the first method, I followed Caughley's (1977) recommendation and used the mean summer home range radius of bears estimated by van Manen (1994) from 3 males and 4 females. In the second method, I used telemetry data from 19 males and 19 females to calculate the distance between telemetry locations and the trapsite of capture for individual bears. I calculated distances from all telemetry locations and summarized male and female distributions separtately.

The second data set that I examined was from previous work performed on the distances of radio-isotope tagged feces from trap sites (Eubanks 1976). In his work, Eubanks (1976) listed the linear distance between tagged feces and the closest and most distant trapsites at which bears were marked with isotopes. I used his distribution of distances to closest trapsites to estimate a conservative distance that bears had traveled. Because sex could not be identified from scats, Eubanks did not list distances separately by sex; therefore, I was unable to analyze male and female distances separately.

The final data set that I examined was the distance between captures of individual bears within GSMNP. I used all available capture events with known locations for this analysis; consequenlty, I analysed capture data from 1967 through 1998. I calculated

distances between all captures of the same individual and separately summarized male and female distributions.

To lessen the influence of rarer long-range movements on the effective study area, I truncated the distribution of distances for all of the above analyses except for the mean home range radius data. I determined where to truncate the distributions by deriving the frequency distribution of distances from the telemetry and capture distance data and then plotting their cumulative frequencies of observed distances. I then truncated these distributions at their horizontal asymptotes, which occurred at approximately the 90^{th} percentile of the observations for both sexes in each data set. Based on these findings, I truncated all distance distributions (including tagged feces distances from trapsites) at 90% for consistency (Appendix B). Also, because of the need for comparison of parameters between the 2 study areas, I took the mean of the combined male and female distances as a single measurement of effective study area size.

Density. I calculated density estimates by dividing abundance estimates by the effective study area size for each study area. I followed the recommendation of Otis et al. (1978) and only used estimates from years that had a resight probability of 10% or higher for all models.

Bait Stations. I used data from bait-station survey routes conducted every summer by GSMNP personnel (Table 2.6) in conjunction with density estimates from this study to perform a correlation analysis in SAS (SAS Inst. Inc. 1990). Rates of bait-station visitation were defined as the proportion of bait sites "hit" by bears on each survey route. Because visitation rates to bait stations were high, many bears likely encountered bait

Table 2.6. Black bear bait-station visitation rates for North Carolina and Tennessee study areas in Great Smoky Mountains National Park, summers 1989 - 1998.

	Black Bear Visitation Rate			
	Southwest Section (NCSA) [1]		Northwest Section (TNSA) [1]	
Year	Unadjusted (f)	Adjusted (f')	Unadjusted (f)	Adjusted (f')
1989	---	---	83.9	182.6
1990	---	---	78.9	155.6
1991	---	---	77.1	147.4
1992	---	---	75.4	140.2
1993	---	---	81.4	168.2
1994	37.50	47.00	63.3	100.2
1995	62.90	99.16	82.8	176.0
1996	53.90	77.44	74.8	137.8
1997	72.80	130.20	83.7	181.4
1998	54.00	77.65	70.8	123.1

[1] TNSA = Tennessee study area; NCSA = North Carolina study area.
[2] $f' = -\ln (1 - (f/100)) \times (100)$, where f is the unadjusted visitation rate and f' is the adjusted visitation rate (Caughley 1977).

stations that had already been "hit" by other bears. Caughley (1977) warned that if visitation rates exceed 20%, trap saturation can have a significant effect and should be addressed; consequently, I used a frequency-density transformation on the data (Caughley 1977):

$$f' = -\ln (1 - (f/100)) \times (100)$$

where: f is the visitation rate and

f' is the transformed visitation rate.

I combined data from survey routes that occurred within or adjacent to each study area boundary (Table 2.6) and compared bait station visitation rates to density for each year and study area. I tested the following null and research hypthotheses:

H_0: Bait-station surveys show no relationship with population estimates.

H_R: Bait-station surveys correlate positively with population estimates.

Results

Remote Cameras. Overall on both study areas, 1,011 sighting opportunities and 3,346 camera nights produced 400 pictures: 368 bears (38 of which I was unable to ascertain the marked status), 25 raccoons (*Procyon lotor*), 6 opossums (*Didelphis virginiana*), and 1 turkey vulture (*Cathartes aura*) (Table 2.4). Thirty-three percent (330/1,011) of the sighting opportunities resulted in usable bear pictures, with the number of camera nights per usable bear picture averaging 10.1 (Table 2.4). The frequency of

resights of marked bears did not differ between camera sites placed at trapsites (2 marked out of 18 total) and those offset from trapsites (2 marked out of 18 total) ($P = 0.699$).

Abundance. I generated abundance estimates from the Lincoln-Petersen model for every year except the first year of trapping on each study area. Point estimates ranged from 311 – 647 bears for the TNSA and from 377 – 521 bears for the NCSA (Table 2.7). Resight probabilities ranged from 4 – 21% on the TNSA and from 6 – 19% on the NCSA. Resight probabilities fell below the minimum acceptable value of 10% during 1991, 1993, and 1994 on the TNSA and during 1995 and 1996 on the NCSA. Lower and upper 95% confidence limits ranged from 33 to 120% of the estimates on the TNSA and from 41 – 120% of the estimates on the NCSA.

I generated abundance estimates with Bailey's Binomial model for 1996 on the TNSA and for 1996 – 1998 on the NCSA. The estimate for the TNSA was 165 bears, and the point estimates for the NCSA ranged from 141 – 279 bears (Table 2.7). The resight probability for the single estimate on the TNSA was 45% and resight probabilities ranged from 25 – 38% on the NCSA. None of the resight probabilities fell below the 10% acceptable minimum. The lower and upper 95% confidence limits on the TNSA were - 19% and + 24% of the abundance estimate, respectively. The upper and lower 95% confidence limits ranged from 21 - 82% of the abundance estimates on the NCSA.

I generated abundance estimates from the back dating method for all years on both study areas (1989 – 1998). Estimates ranged from 178 – 262 bears on the TNSA and from 178 – 229 bears on the NCSA (Table 2.7). No resight probabilities or confidence intervals could be calculated using this method.

Table 2.7. Black bear abundance estimates and related data for North Carolina and Tennessee study areas in Great Smoky Mountains National Park, summers 1989 - 1998.

Year	Study Area[1]	Lincoln/Petersen N[2]	Lincoln/Petersen Lower 95% CI	Lincoln/Petersen Upper 95% CI	Lincoln/Petersen p[3]	Camera Resight N[2]	Camera Resight Lower 95% CI	Camera Resight Upper 95% CI	Camera Resight p[3]	Back Dating N[2]	Jolly/Seber N[2]	Jolly/Seber Lower 95% CI	Jolly/Seber Upper 95% CI	Jolly/Seber p[3]
1989	TNSA	---	---	---	---	---	---	---	---	213	---	---	---	---
1990	TNSA	373	202	697	0.10	---	---	---	---	195	389	188	1,227	0.09
1991	TNSA	532	233	1,172	0.06	---	---	---	---	195	249	145	606	0.19
1992	TNSA	311	168	581	0.15	---	---	---	---	197	292	169	700	0.16
1993	TNSA	647	204	1,232	0.04	---	---	---	---	178	167	93	426	0.15
1994	TNSA	345	162	729	0.06	---	---	---	---	220	224	151	429	0.27
	NCSA	---	---	---	---	---	---	---	---	178	---	---	---	---
1995	TNSA	315	208	536	0.19	---	---	---	---	242	283	203	490	0.31
	NCSA	377	165	831	0.06	---	---	---	---	191	856	343	3,656	0.05
1996	TNSA	456	285	752	0.18	165	134	221	0.45	224	411	271	799	0.18
	NCSA	521	256	1,054	0.09	221	162	403	0.25	205	532	269	1,557	0.10
1997	TNSA	495	326	842	0.15	---	---	---	---	262	296	205	565	0.40
	NCSA	480	270	881	0.11	279	220	407	0.29	229	258	152	652	0.31
1998	TNSA	521	343	886	0.21	---	---	---	---	227	---	---	---	---
	NCSA	414	244	721	0.19	141	112	201	0.38	208	---	---	---	---
Mean (SD)[4]	TNSA	447	(79.5)			165	(---)			235 (15.4)	304	(67.7)		
	NCSA	447	(33.0)			218	(54.5)			201 (16.9)	258	(137.0)		

[1]TNSA = Tennessee study area; NCSA = North Carolina study area.
[2]N=estimated abundance from model.
[3]p=resight probability.
[4]Averages for 1994 to 1998 and estimates with resight probability 10%.

Model selection output from program Jolly indicated that models A and B were the best fitting models (had non-significant *P*-values) on the TNSA and models A and A' were the best fitting for the NCSA. Because of uncertainties regarding violation of assumptions under models A' (no immigration) and B (constant survival), I generated abundance estimates using model A for 1990 – 1997 on the TNSA and from 1995 – 1997 on the NCSA. Estimates ranged from 167 – 411 bears on the TNSA and from 258 – 856 bears on the NCSA (Table 2.7). Resight probabilities ranged from 9 – 40% on the TNSA and from 5 – 31% on the NCSA. Resight probabilities fell below the acceptable minimum value of 10% during 1990 on the TNSA and during 1995 on the NCSA. Lower and upper 95% confidence intervals ranged from 28 – 215% of the abundance estimates on the TNSA and from 41 – 327% on the NCSA.

Effective Study Area. Distances traveled by bears between capture locations ranged from 0 – 15,455 m for females and 0 – 26,434 m for males (Appendix B). Distances between radio-isotope tagged scats and the nearest possible point of capture for bears ranged from 500 – 9,500 m for both sexes combined (Appendix B). Distances between telemetry locations and point of capture for bears ranged from 0 – 9,575 m for females and 0 – 59,921 m for males (Appendix B). Truncation of these distance distributions at 90% in conjunction with average home range radii of female and male bears resulted in effective study area buffer radii estimates that ranged from 1,300 – 2,250 m for female bears and from 3,750 – 7,500 m for male bears (Table 2.8). The mean of male and female buffer radii estimates ranged from 2,525 – 4,875 m and overall averaged 3,463 m (Table 2.8). I used the overall average radius estimate to generate the area of use

Table 2.8. Summary of parameters used to calculate the buffer radius to delineate the effective study area for and area used by black bears in Great Smoky Mountains National Park, summers 1989 - 1998.

Method	Distance (meters)		
	Female	Male	Average
Home Range Radius[a]	1,300	3,750	2,525*
Recapture Distance[b]	1,600	4,800	3,200
Scat Distance[c]	---	---	3,250
Telemetry Distance[d]	2,250	7,500	4,875
Average	1,717	5,350	3,463[†]

[a]Average radius from summer home range sizes as calculated by van Manen 1994.
[b]Length determined by truncating the distribution of distances between bear recaptures at 90% as calculated in this study.
[c]Length determined by truncating the distribution of distances between radio isotope tagged bear scats and the nearest trapsite at 90% as calculated by Eubanks 1976.
[d]Length determined by truncating the distribution of distances between bear telemetry locations and site of capture at 90% as calculated in this study.
*Buffer distance used to delineate effective study area for density estimation.
[†]Buffer distance used to delineate area used by bears for study area comparisons.

around trapsites for study are delineation and used the average home range radius to calculate effective study area sizes for density estimation (see Discussion). Based on these distances, study areas totaled 357.7 and 400.5 km^2 for the TNSA and NCSA, respectively (Figure 2.1) and effective study areas totaled 252 and 274 km^2 for the TNSA and NCSA, respectively.

Density. After discarding abundance estimates that had resight probabilities less than 10%, I generated density estimates from the Lincoln-Petersen model results for 1990, 1992, and 1995 – 1998 on the TNSA and 1997 – 1998 on the NCSA. Lincoln/Petersen densities varied from 0.39 – 1.46 bears/km^2 in the TNSA and from 0.88 – 0.93 bears/km^2 in the NCSA (Table 2.9). I generated density estimates from Bailey's Binomial model results for 1996 in the TNSA and 1996 – 1998 on the NCSA. The Bailey's Binomial densities equaled 0.46 bears/km^2 for the TNSA and varied from 0.35 – 0.70 bears/km^2 on the NCSA (Table 2.9). I generated density estimates from the back dating method for all years. Back dating densities varied from 0.50 – 0.73 bears/km^2 on the TNSA and 0.44 – 0.57 bears/km^2 on the NCSA (Table 2.9). After discarding abundance estimates that did not meet the resight probability criterion, I generated density estimates from the Jolly/Seber model results for 1991 – 1997 on the TNSA and 1996 – 1997 on the NCSA. Jolly/Seber densities varied from 0.47 – 1.15 bears/km^2 on the TNSA and 0.64 – 1.33 bears/km^2 on the NCSA (Table 2.9). Average densities from all models varied from 0.49 – 1.05 bears/km^2 on the TNSA and 0.44 – 0.80 bears/km^2 on the NCSA (Table 2.9). Back-dating estimates showed a stable density of bears in the TNSA from 1989 – 1992, followed by a drop in density during 1993, then an increasing trend to

Table 2.9. Black bear density estimates (bears/km^2) for North Carolina and Tennessee study areas in Great Smoky Mountains National Park, summers 1989 - 1998.

		Lincoln / Petersen			Camera Resight			Back Dating	Jolly/Seber		
Year	Study Area[1]	N	Lower 95% CI	Upper 95% CI	N	Lower 95% CI	Upper 95% CI	N	N	Lower 95% CI	Upper 95% CI
1989	TNSA	---	---	---	---	---	---	0.85	---	---	---
1990	TNSA	1.48	0.80	2.77	---	---	---	0.77	---	---	---
1991	TNSA	---	---	---	---	---	---	0.77	0.99	0.58	2.40
1992	TNSA	1.23	0.67	2.31	---	---	---	0.78	1.16	0.67	2.78
1993	TNSA	---	---	---	---	---	---	0.71	0.66	0.37	1.69
1994	TNSA	---	---	---	---	---	---	0.87	0.89	0.60	1.70
	NCSA	---	---	---	---	---	---	0.65	---	---	---
1995	TNSA	1.25	0.83	2.13	---	---	---	0.96	1.12	0.81	1.94
	NCSA	---	---	---	---	---	---	0.70	---	---	---
1996	TNSA	1.81	1.13	2.98	0.65	0.53	0.88	0.89	1.63	1.08	3.17
	NCSA	---	---	---	0.84	0.59	1.47	0.75	1.94	0.98	5.68
1997	TNSA	1.96	1.29	3.34	---	---	---	1.04	1.17	0.81	2.24
	NCSA	1.75	0.99	3.22	1.01	0.80	1.49	0.84	0.94	0.55	2.38
1998	TNSA	2.07	1.36	3.52	---	---	---	0.90	---	---	---
	NCSA	1.51	0.89	2.63	0.53	0.41	0.73	0.74	---	---	---
Mean (SD)[2]	TNSA	1.77	(0.32)		0.65	(---)		0.93 (0.06)	1.20	(0.27)	
	NCSA	1.63	(0.12)		0.79	(0.20)		0.73 (0.06)	0.94	(0.50)	

[1]TNSA = Tennessee study area; NCSA = North Carolina study area.
[2]Averages for 1994 to 1998 only.

slightly higher densities from 1994 – 1997, and finally a drop back down to pre-1993 densities in 1998 (Figure 2.4). Results for the NCSA showed similar trends from 1994 – 1998 (Figure 2.5). Lincoln/Petersen estimates indicated decreasing densities from 1990 to 1992 and then a dramatic increase in density from 1995 to 1998 on the TNSA. The 2 estimates on the NCSA showed a decrease from 1997 to 1998. Because the trends on the TNSA were not mirrored by any of the other models, I attributed them to model imprecision associated with the low resight rates in later years. Jolly/Seber estimates fluctuated markedly and tended to be higher than the back dating and Bailey's Binomial model estimates. Bailey's Binomial model results mirrored those of the back dating method from 1996 – 1998 on the NCSA, but only had a single point in 1996 on the TNSA, which fell below the back dating estimate for that year.

Bait Stations. The correlation analysis between the adjusted bait station index and the Lincoln/Petersen, Bailey's Binomial, and Jolly/Seber, density estimates yielded non-significant results (Appendix C). The adjusted bait station index and back dating density estimates were significantly correlated ($P = 0.0097$; $R^2 = 0.64$) (Appendix C) (Fig. 2.6).

Discussion

The models for estimation of population size used in this study generated varying results for many of the years investigated (Figures 2.4 and 2.5); several factors led to this situation. The most salient difference occurred between the Lincoln/Petersen model and the other models. The Lincoln/Petersen model consistently estimated higher numbers of

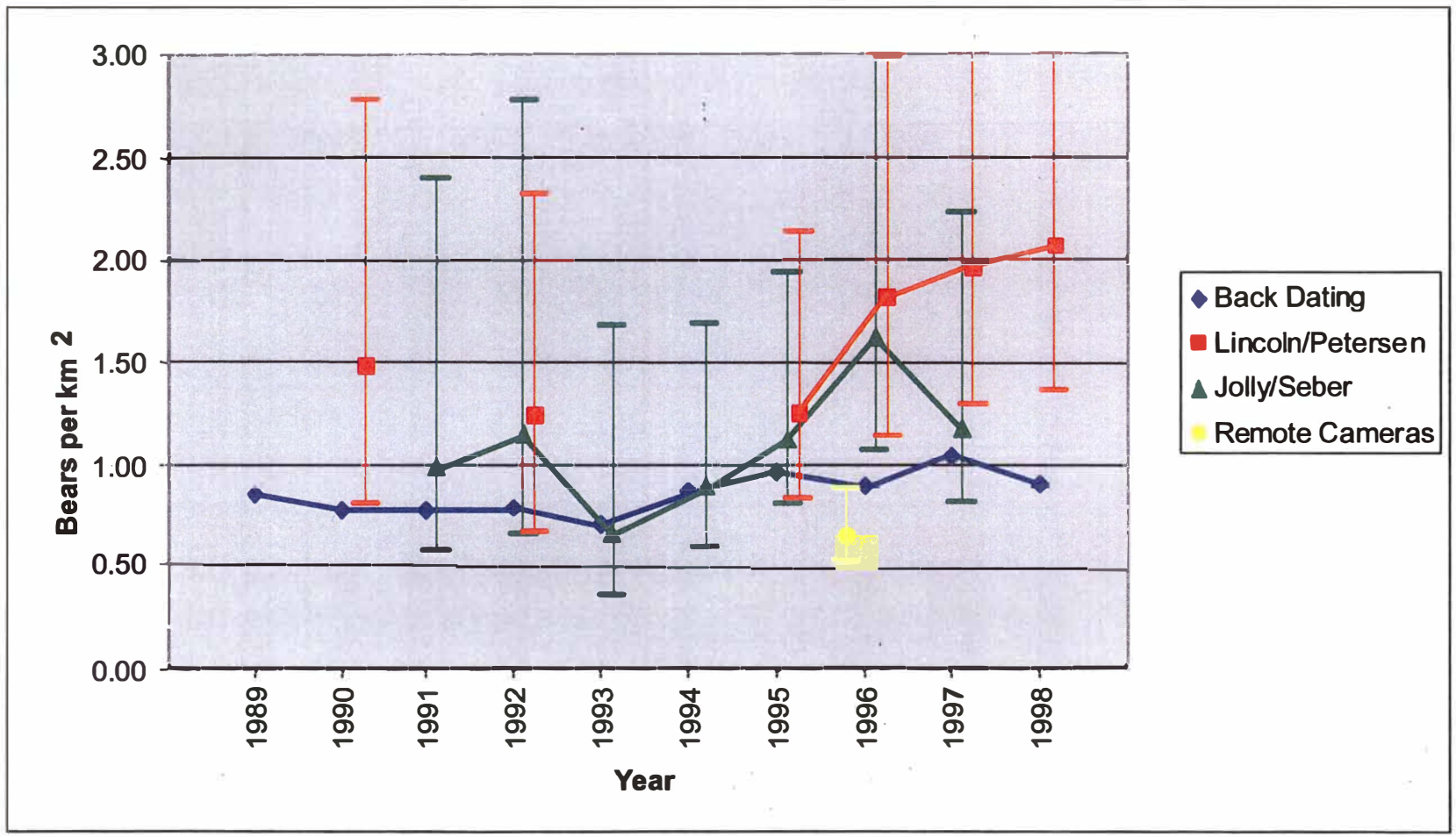


Figure 2.4. Black bear density estimates with 95% confidence intervals for Tennessee study area in Great Smoky Mountains National Park, summers 1989 - 1998.

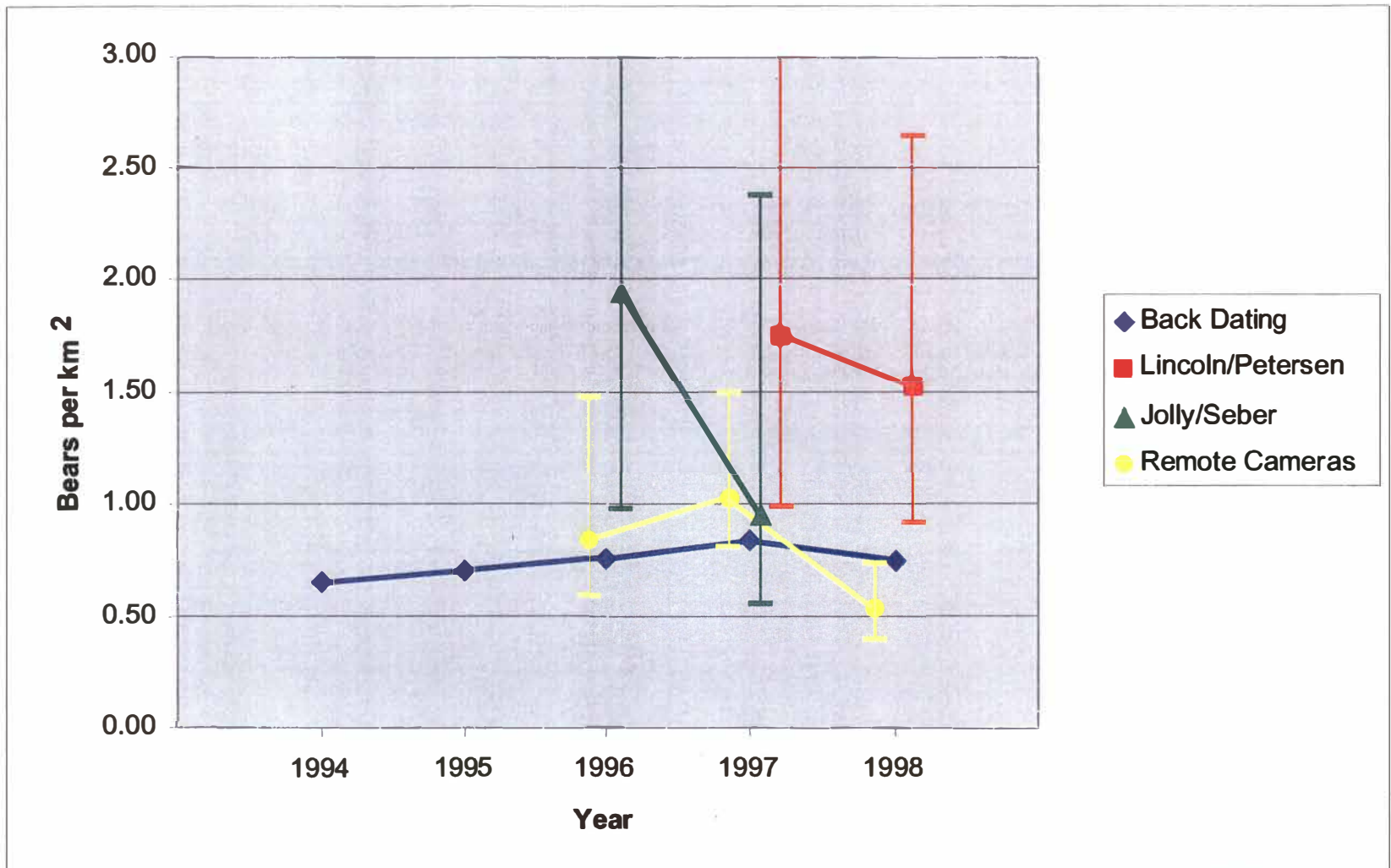


Figure 2.5. Black bear density estimates with 95% confidence intervals for North Carolina study area in Great Smoky Mountains National Park, summers 1994 - 1998.

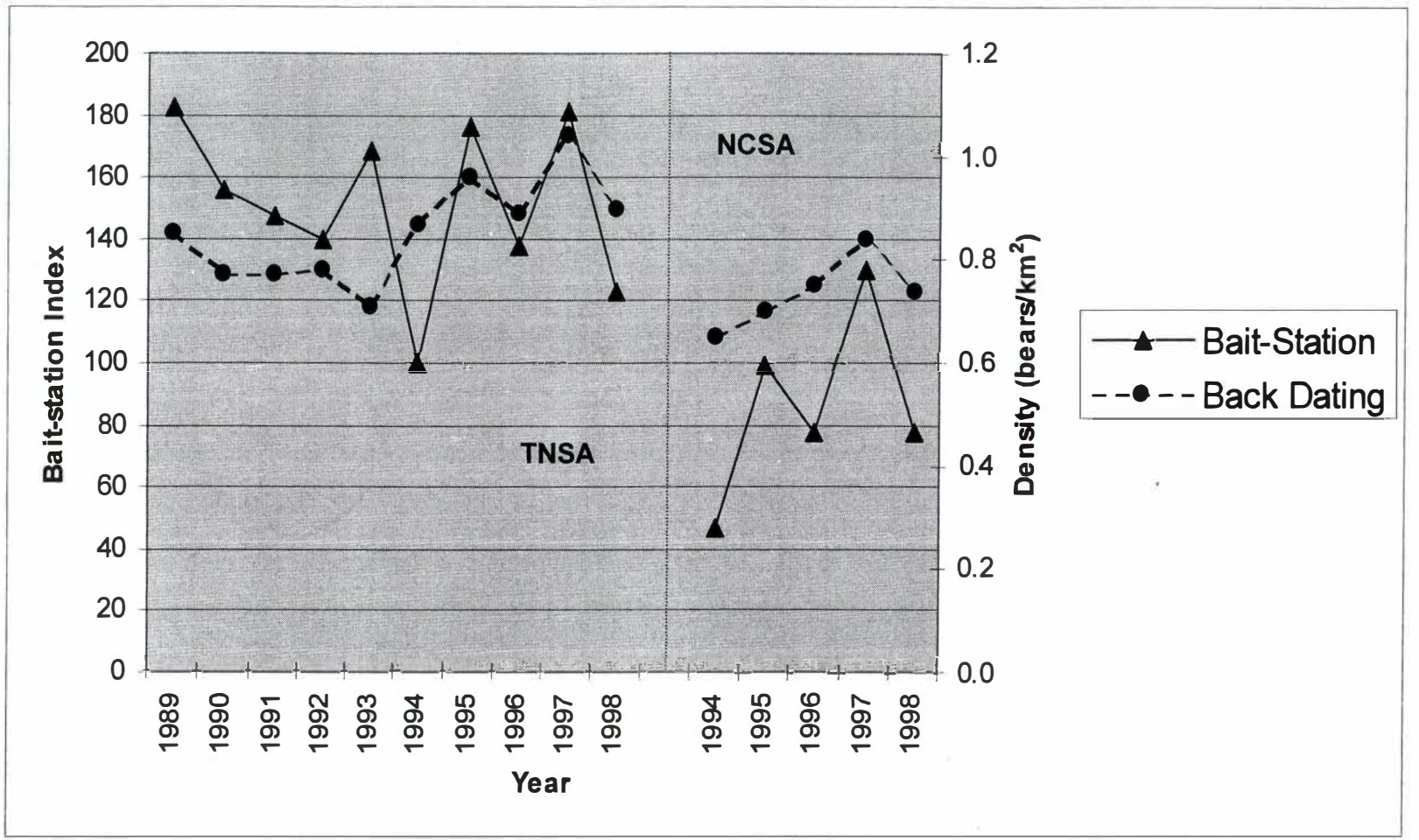


Figure 2.6. Density estimates from back dating model and adjusted bait-station visitation rates for North Carolina and Tennessee study areas in Great Smoky Mountains National Park, summers 1989 - 1998.

bears than any of the other models, except for the Jolly/Seber model during years of low resight rates (see below). I believe that this overestimation resulted from violation of model assumptions. The manner in which bears were trapped over 2 years resulted in violation of the population closure assumption. There was little evidence to suggest that marked and unmarked bears exhibited different rates of death or emigration, and even though yearlings and other bears may have been added to the population each year, recording the estimate for the second year of the model period captured their presence without bias (Pollock et al. 1990). However, if mortality or emigration occurred in conjunction with immigration, model estimates would have been biased high. Additionally, another assumption violation that may have occurred was that of equal catchability among individuals. It was evident during trapping that once caught bears became "trap smart." Even though previously captured bears would continue to visit trapsites, it was difficult to recapture them. Pedersen (1995) investigated this phenomenon in GSMNP and concluded that even though trap response was evident, the length of trapping (14 days) reduced trap response by allowing multiple opportunities to capture "trap smart" bears. Even so, Coley (1995) showed that the average time interval between captures of bears in GSMNP was 1.8 and 2.1 years for males and females, respectively. Consequently, recapture were biased low for the Lincoln/Petersen model, which utilizes only 2 consecutive years of data (i.e., the average bear was not likely to be recaptured between consecutive sampling periods). The net result was that marked bears were resighted at a lower rate than their proportion in the population, biasing the

estimates high. Because of these biases, I do not believe that the Lincoln/Petersen model provided accurate estimates of the population size of bears in GSMNP.

Fluctuations in Lincoln/Petersen and Jolly/Seber model results were caused by low resight probabilities for several years. Resight rates fell below the minimum acceptable value of 10% during 5 years for the Lincoln/Petersen model and during 2 years for the Jolly/Seber model. Additionally, resight rates exceeded 20% during only 1 year for the Lincoln/Petersen model and 4 years for the Jolly/Seber model (Table 2.8). Years that showed noticeably large fluctuations in estimation of population size corresponded to years with low resight rates (i.e., 1990 for the Lincoln/Petersen model on the TNSA; 1997 for the Lincoln/Petersen model on the NCSA; 1992 and 1996 for the Jolly/Seber model on the TNSA; and 1996 for the Jolly/Seber model on the NCSA). The remote camera data used in Bailey's Binomial model generated relatively high (25 – 45%) resight rates and, consequently, generated more robust estimates for most years than the Lincoln/Petersen and Jolly/Seber models. Low resight rates for the Lincoln/Pedersen model could be explained by trap response from "trap smart" bears; however, for the Jolly/Seber model, which used data from multiple years, a different explanation was necessary.

Because of the large number of bear captures each year (27 – 135), I do not believe that the low resight rates were attributed to small sample sizes. Instead, I believe that sub-optimal sampling caused the low resight rates. The ideal study design for mark-recapture is one that minimizes the perimeter to area ratio and buffer size of the study area by approximating a circle or square in shape (Figure 2.7), covers a large enough area

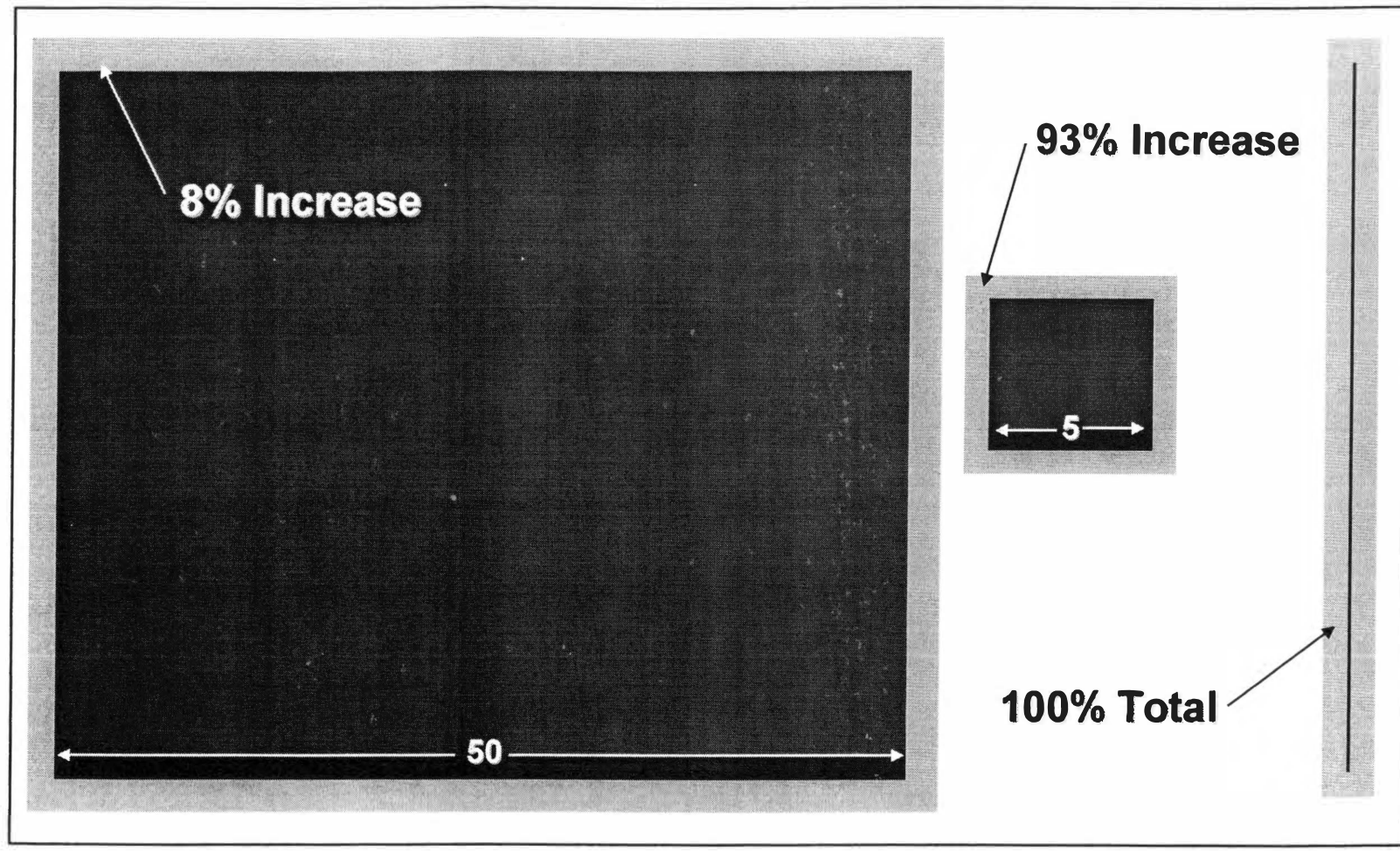


Figure 2.7. Representation of increasing buffer area size (light gray shading) as a percentage increase around trapping grids of different size and shape (dark shading) (adapted from White et al. 1982).

to sample at least 50 individuals, and saturates the entire study area with at least 4 trapsites per home range (Otis et al. 1978, White et al. 1982). If accomplished, such a design results in high capture and resight probabilities that should be equal for all individuals within the study area, unless temporal or behavioral response is significant. The most significant departure from optimal conditions during this study was the elongated nature of the study areas caused by the near linear, clumped distribution of trapsites on the landscape. The logistics of foot access to the study areas and the desire of the National Park Service to survey large portions of GSMNP necessitated such a distribution. The effect of this placement of trapsites was large study areas with non-contiguous segments and high perimeter to area ratios (Figure 2.1). These attributes resulted in nearly linear study areas consisting mostly of buffer areas that were not sampled intensively (Figure 2.6); this, in turn, contributed significantly to low resight rates. The best way to have increased resight rates would have been to reduce study areas to sizes that could have been intensively sampled with available manpower, or greatly increase the number of trapsites. Neither of these options was realistically obtainable for this study. Consequently, resight rates were low, variance around population size estimates was large, and model results fluctuated widely during some years.

The back dating method produced a conservative baseline of population size in both study areas. As expected, back-dating yielded estimates that tended to be lower and fluctuated less than those from other models. A drawback to the back dating model was the inability to calculate confidence intervals around the point estimates, making it impossible to gauge precision or robustness of estimates. The use of a simple linear

regression to estimate the population size in the final 3 years for each study area proved workable and extended the estimates to the full 10 and 5 years of data for the TNSA and NCSA, respectively. This procedure enhanced the usefulness of the back dating method as a baseline for the entire period of the study.

The remote cameras generated large sample sizes and yielded the most precise estimates of any model for the years in which they were deployed. Because estimates generated by Bailey's Binomial model from the remote camera data fell below the back-dating estimates on 2 occasions, I had some concern that they were underestimating the true population size. The most likely cause of underestimation was the habitual return to camera sights by some marked bears. Many photographs, particularly of a radio-collared female on Parson's Branch Trail on the TNSA in 1996, showed the same individual "hitting" multiple camera sights on every resight occasion. If this "trap happy" behavior was exhibited preferentially by marked bears, presumably because they were conditioned to search for bait along the traplines, then the estimates would be biased low. However, comparison of camera sights placed at trapsites, which should have been preferentially detected by marked bears under the above assumptions, versus those offset from trapsites resulted in identical hit rates of marked and unmarked bears. The lack of individually discernable marks on bears made it difficult to determine if a handful of "trap smart" bears were accounting for most of the resights. Ocular assessment of the photos did not support this contention, so I assumed that marked and unmarked bears exhibited "trap smartness" equally and that this behavior had little affect on the accuracy of the estimates. Substantial numbers of hits by single bears, however, could have erroneously increased

precision of the estimates by increasing sample sizes to artificially high levels (Seber 1982). The use of expensive, infrared-triggered, multiple-shot cameras would have enabled a more complete assessment of the behavior and of individual bears (Bowman et al. 1996, Grogan and Lindzey, in press, Mace et al. 1994). Overall, because of the short time between capture and resight and the large sample sizes, I believed that the remote camera technique minimized population closure violations and yielded reasonable estimates.

Back dating estimates provided good trend data on minimum densities of bears, which tended to increase through time on both study areas. Density estimates from the remote camera data showed similar trends during years when estimates were generated, but large variances associated with Lincoln-Petersen and Jolly-Seber estimates made it difficult to discern clear trends from these models. I concluded that the back dating and remote camera estimates depicted meaningful trend information, but most likely were biased low. I also concluded that the Lincoln-Petersen estimates were biased high (because of assumption violations discussed earlier) and generally did not portray useful trend information (because of large variance around estimates). Lastly, I concluded that the Jolly-Seber estimates were the least biased, but suffered from large variance because of low resight rates in most years. Estimates of density on the TNSA tended to be higher than those on the NCSA; however, densities from both study areas fell below Coley's (1995) estimates for 1973 – 1991, above McLean's (1991) estimates for 1973 – 1987, and in the upper-most range for other studies across North America (see Clark 1991, Coley 1995, Garshelis 1994, McLean 1991).

The lower estimates of density on the NCSA compared to the TNSA were due in part to slightly fewer bears in the NCSA population estimates, but predominantly were the result of the larger size of the NCSA effective study area. The layout of traplines and trapsites on the NCSA was done in such a manner as to mirror those on the TNSA. However, because of logistic constraints, the lines on the NCSA were more dispersed than those on the TNSA, resulting in a larger effective study area. To discern how increasing length of the buffer radius influenced study area size (and consequently density), I calculated hypothetical effective study area sizes based on buffering radii ranging from 500 – 5,000 m (Fig. 2.8). This process revealed that, proportionally, the NCSA increased (or decreased) in size at a faster rate than the TNSA, except at extremely small and large radii (Fig. 2.8). It also showed that the proportional rate of increase slowed markedly for each study area at radii lengths ≥ 3,500 m (Fig. 2.8). I believe that the effective study area calculated in this study more accurately represented the zone of sampling around trapsites than the study areas defined by McLean (1991) and Coley (1995). Consequently, density estimates generated from this study should more accurately reflect true values.

The failure of the bait-station index to correlate with any of the population estimates, except the back dating method, was discouraging. Many state agencies and other management institutions use bait stations to track relative population trends in black bears (Garshelis 1991). If bait stations truly do not correlate with population size, then managers have been wasting resources gathering this type of information and may have been making unfounded management decisions. So, then, why did the bait-stations

Table 2.10. Influence of buffer distance on size of effective study area for black bears in Great Smoky Mountains National Park, summers 1989 - 1998.

	North Carolina Study Area		Tennessee Study Area		
Buffer Distance (m)	Area (km^2)	% Increase	Area (km^2)	% Increase	% Difference*
500	32.2	---	30.6	---	5.2
1,000	83.4	159.0	80.1	161.8	4.1
1,500	143.5	72.1	134.4	67.8	6.8
2,000	212.2	47.9	191.4	42.4	10.9
2,500	285.4	34.5	249.2	30.2	14.5
3,000	359.9	26.1	305.1	22.4	18.0
3,500	430.3	19.6	361.9	18.6	18.9
4,000	499.9	16.2	420.6	16.2	18.9
4,500	571.0	14.2	481.6	14.5	18.6
5,000	643.6	12.7	545.0	13.2	18.1

*As proportion of Tennessee Study Area: (North Carolina Study Area - Tennessee Study Area) / Tennessee Study Area.

correlate with back dating estimates only? I believe that the main reasons for the lack of correlation with other estimates was the relatively low resight rates and large variances associated with the Lincoln-Petersen and Jolly/Seber results and the small number of data points used the 3 other models. Consequently, power to detect correlations among the data was low. Overall, these analyses suggest that, in the southern Appalachians, bait stations do, at least, generate useful information regarding trends in the minimum number of bears residing in a given area. Further work based on longer time frames and larger sample sizes is needed to more robustly ascertain if bait-stations correlate with other abundance estimates.

CHAPTER III

POPULATION COMPARISON

Introduction

Modern bear management theory is predicated upon knowing how many individuals (either absolutely or relatively) are present in a population and how they respond to stimuli, both natural and anthropogenic. Once these responses are uncovered and their mechanisms understood, managers are able to manipulate bear populations to achieve a desired end. If a population is growing too large, it can be reduced; if it is becoming too small, it can be increased; and if it is at an appropriate level, it can be maintained. Managers are always at the mercy of variation inherent in biological systems and uncontrollable natural events, but within these constraints, they can hasten recoveries and dampen irruptions, attempting to keep populations within limits acceptable to humans around them (i.e., cultural carrying capacity).

Unfortunately, theory and practice often are far removed from one another. Research rarely provides accurate and timely information on bear population parameters, forcing managers to make decisions based on general trends and uncalibrated indices. Lacking knowledge of fundamental parameters like abundance and density, researchers are unable to correlate population responses to stimuli and cannot attribute mechanisms to the process. Consequently, great effort and research has been dedicated to estimating population parameters of bears, with mixed success.

In the southern Appalachians, GSMNP has served as a center of bear research since 1967, with most research focused on elucidating the dynamics of black bear ecology. The research design has been based on annual summer trapping and winter denwork. This design has resulted in a long-term data set (Pelton and van Manen 1996) that contains > 2,500 bear captures and spans 34 years (1968 – 2001). The data set has been formed from numerous smaller studies, each conducted for 2-4 years. Trapping efforts did not become totally consistent until 1989 when 8 traplines were permanently established. These 8 lines were trapped at the same time of year with nearly equal effort each year through 1998. Prior to this standardization, trapping efforts within the study area occasionally moved among different trails to suit the needs of the shorter, individual projects. This shifting of trapping and tagging to new traplines led to some inconsistencies and missing data that hindered more accurate work on estimation of population size and demographics.

Bear investigations in the GSMNP have been restricted to portions of the northwestern quadrant, which represents < 20% of the total area. Bears from other areas within GSMNP may differ ecologically and demographically from those in the northwestern quadrant. For example, the southwestern shows consistently lower bait-station visitation compared to the northwestern quadrant (Bill Stiver, GSMNP, unpubl. data). This lower visitation rate coincides with circumstantial evidence of poaching activity throughout the area. Consequently, resource managers hypothesize that the density of bears in the southwestern quadrant may be the lowest in GSMNP. These

circumstantial data suggest that extrapolations from research conducted in the northwestern quadrant to the entire Park, or the region, may be tenuous.

In this study, I established a new study area and combined data gathered from it with data from the traditional study area to obtain more reliable population characteristics for black bears in GSMNP. Through comparisons between the new study area and the traditional one, I sought to determine if bear population parameters were uniform throughout GSMNP, and presumably the region, or varied locally. Through these methods, I sought to provide a better understanding of bear population characteristics and demographics. The specific objective of this study was to compare bear population sex ratios, age structures, body sizes (weights), litter sizes, survival rates, and densities for the northwestern and southwestern quadrants of GSMNP. Through such comparisons I sought to ascertain if population dynamics of bears varied between 2 study areas due to poaching or other factors.

Study Area

I defined 2 study areas within GSMNP by buffering trapsites on each side of the Park with an estimated effective sampling radius (see Chapter II - Methods) and taking the cumulative area of these buffers (Fig. 2.1). Although this procedure resulted in 2 disjunct areas on each side of the Park, I combined each pair to make comparisons across the intended study areas. This grouping also bolstered analyses by increasing sample sizes and sampling areas. The salient characteristics of these 2 study areas are described in the following sections.

North Carolina Study Area. The NCSA was established for this study in summer 1994 and was active for 5 years, through summer 1998. This study area totaled 400 km^2 in size (19% of the Park) and consisted of 8 traplines that stretched eastward from the southwestern boundary of GSMNP to highway 441 and southward from the North Carolina-Tennessee border to Fontana Lake (Fig. 2.1). This portion of GSMNP is remote and has no road system; consequently, the only means of access was via boat on Fontana Lake or hiking on backcountry trails. Because of these factors, visitor use of the area is low compared with other, more easily accessible, areas of GSMNP.

Characteristics of the NCSA varied slightly in some attributes compared to the Park as a whole (Tables 3.1, 3.2, and 3.3). Elevation ranged from 387 m to 1,929 m and averaged 949 m (Fig. 3.1, Table 3.1). Prominent cover types included cove hardwood, mixed mesic hardwood, and mesic oak; these cover types cumulatively covered nearly three quarters of the study area (Fig. 3.1, Table 3.2). Slope averaged 23.8° and tended to be greatest at higher elevations (Fig. 3.1, Table 3.1). Owing to the direction of the main ridgelines, aspects tended toward the south and west (Fig. 3.1, Table 3.3). Based on the analyses of van Manen (1994), average bear habitat use probabilities were similar for males and females on the NCSA and exhibited geographic pattern (Fig 3.1, Table 3.1). Female habitat use probabilities were highest in higher elevations and remote areas, whereas male habitat use probabilities were highest in lower elevations (Fig. 3.1).

Tennessee Study Area. The TNSA was originally established in 1968 and has been continuously sampled, in various forms, to the present. Because of differing objectives for the studies that have been conducted on the TNSA, the specific study areas,

Table 3.1. Summary of habitat characteristics for black bear study in Great Smoky Mountains National Park, 1994 – 1998.

Habitat Characteristic	GSMNP				NC Study Area				TN Study Area			
	Mean	STD	Min	Max	Mean	STD	Min	Max	Mean	STD	Min	Max
Aspect (°)[1]	---	---	---	---	---	---	---	---	---	---	---	---
Elevation (m)	1,014	345	266	2027	949	262	387	1929	771	235	329	1552
FHUP	31.8	24.0	0.0	97.0	39.3	28.2	0.0	96.0	34.2	21.4	0.0	97.0
MHUP	43.2	19.8	0.0	96.0	41.2	18.5	1.0	93.0	54.7	19.6	1.0	95.0
Forest Type[2]	---	---	---	---	---	---	---	---	---	---	---	---
Slope (°)	23.2	8.9	0.0	64.5	23.8	7.6	0.0	65.1	20.9	9.1	0.0	58.6

[1]See Table 3.3 for summary of aspect values.
[2]See Table 3.2 for summary of forest types.

Table 3.2. Proportion of forest types within Great Smoky Mountains National Park and the North Carolina and Tennessee bear study areas, (from MacKenzie 1991, 1993).

Forest Type	GSMNP (%)	NC Study Area (%)	TN Study Area (%)
Spruce – Fir	2.3	0.5	0.0
Northern Hardwood	9.4	5.1	1.7
Cove Hardwood	33.4	33.0	20.8
Mesic Oak	10.3	18.0	3.0
Mixed Mesic Hardwood	16.0	22.6	17.0
Tulip Poplar	2.7	0.3	7.7
Xeric Oak	10.0	9.6	22.0
Pine – Oak	2.4	4.9	2.4
Pine	11.2	5.8	23.6
Open	2.3	0.2	1.8

Table 3.3. Distribution of aspects within Great Smoky Mountains National Park and the North Carolina and Tennessee bear study areas.

Aspect	GSMNP (%)	NC Study Area (%)	TN Study Area (%)
North (337.6° – 22.5°)	12.3	8.6	15.1
Northeast (22.6° – 67.5°)	11.6	8.5	12.5
East (67.6° – 112.5°)	11.7	12.2	10.6
Southeast (112.6° – 157.5°)	12.1	14.7	11.1
South (157.6° – 202.5°)	13.2	17.9	10.7
Southwest (202.6° – 247.5°)	12.1	13.2	10.5
West (247.6° – 292.5°)	14.0	14.1	14.2
Northwest (292.6° – 22.5°)	13.0	10.8	15.3

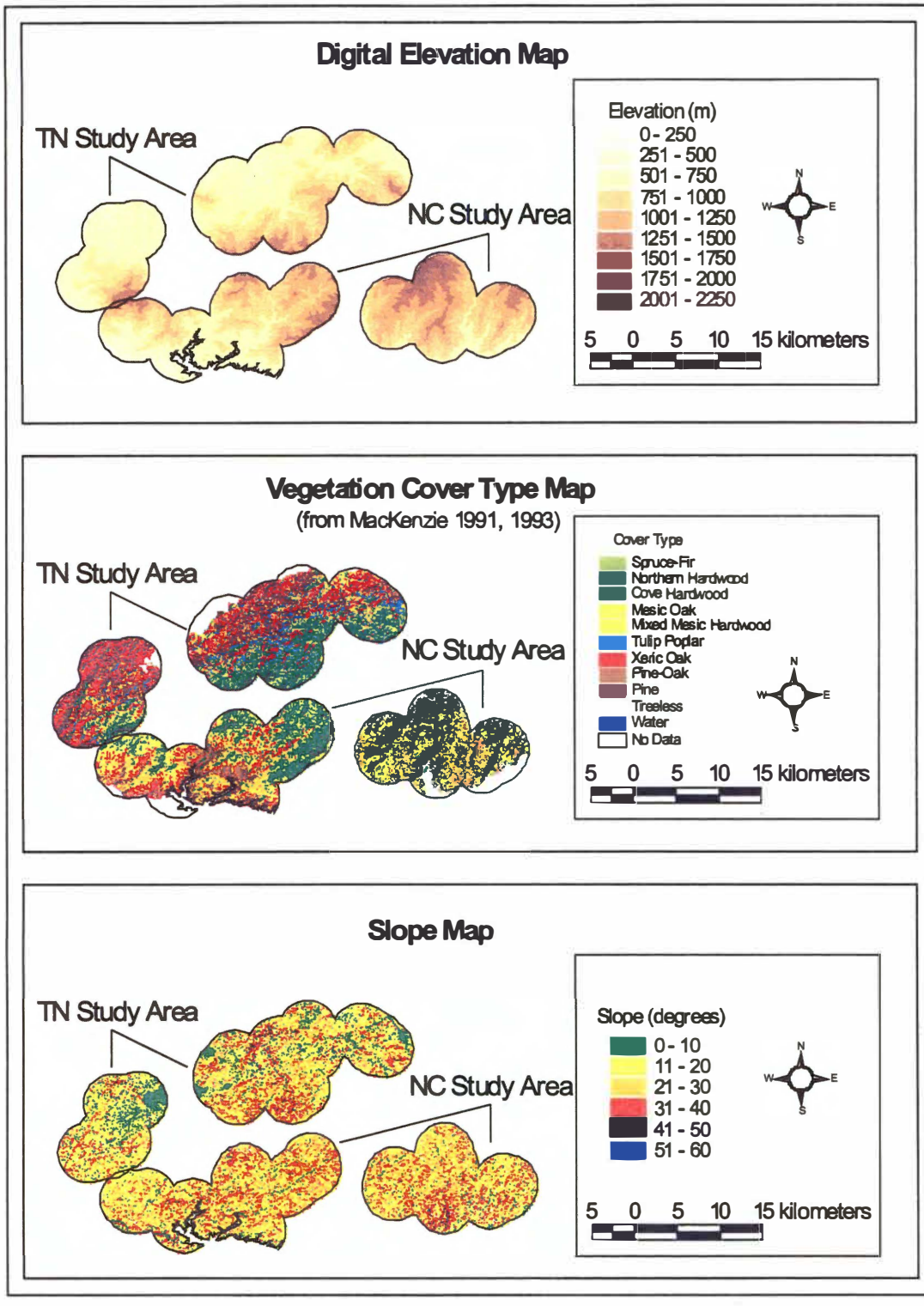


Figure 3.1. Geographic Information System (GIS) maps of North Carolina and Tennessee study areas in Great Smoky Mountains National Park, 1994 – 1998.

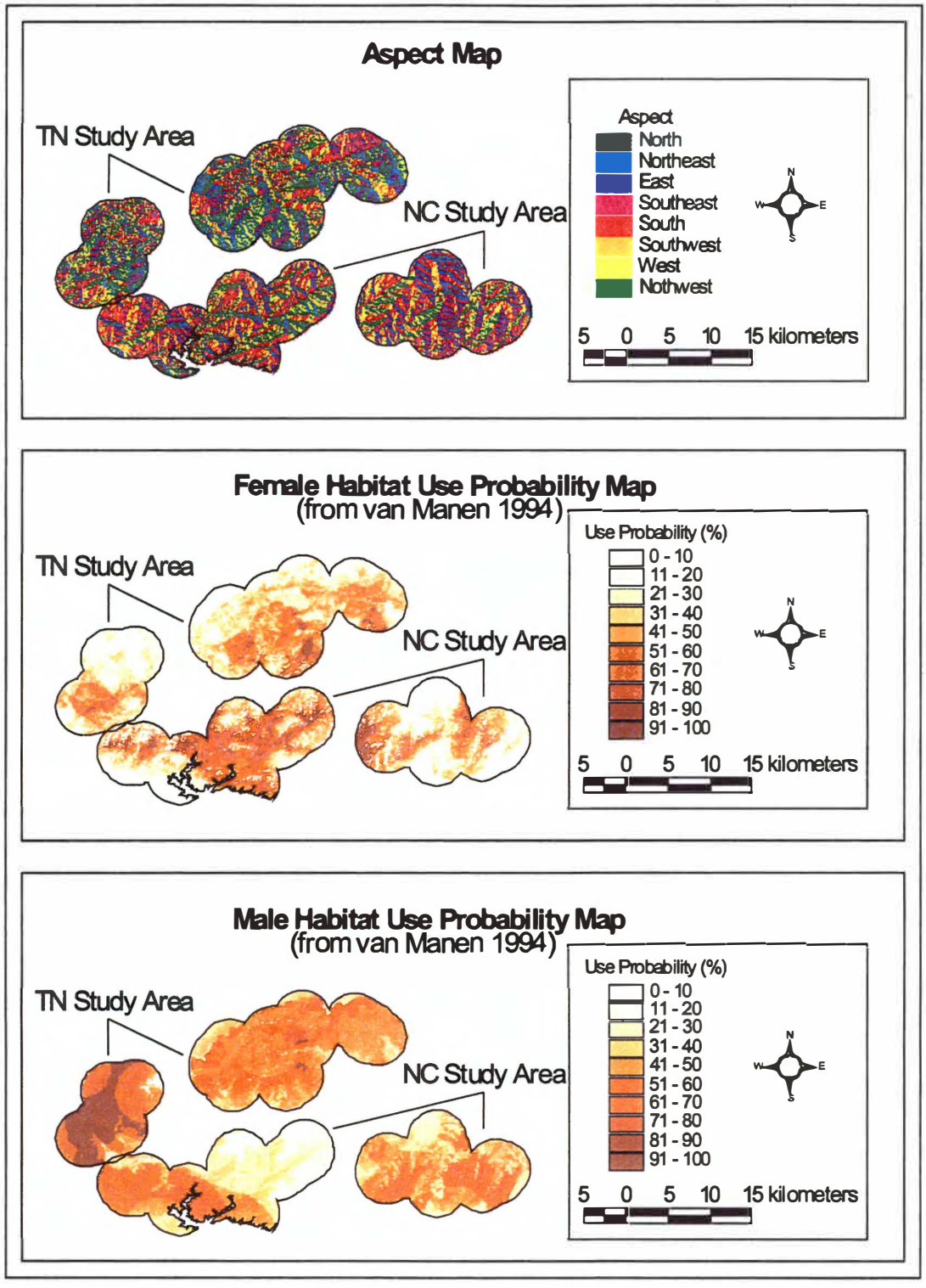


Figure 3.1. Cont.

traplines, and trapsites have changed slightly throughout the years. The general location for all of these studies has been the area stretching eastward from the northwestern boundary of GSMNP to highway 441 and northward from the North Carolina-Tennessee border to the northern boundary of the Park (Fig. 1.1). Several paved roads traverse this portion of GSMNP and provide access to popular areas such as Cades Cove, Tremont, and Sugarlands; consequently, visitor use rates are high.

Within the general locale of the TNSA, the study area for this investigation was limited to 8 traplines that were consistently sampled from summer 1989 to summer 1998 (Fig. 2.1). This area totaled 358 km^2 (17% of the Park) and was similar in characteristics to the entire Park, except that it tended to be lower in elevation and contain a higher percentage of the xeric oak and pine cover types (Tables 3.1, 3.2, and 3.3). Elevation ranged from 329 m to 1,552 m and averaged 771 m (Fig. 3.1, Table 3.1). More than two thirds of the TNSA was covered by 3 dominant cover types: pine, xeric oak, and cove hardwood (Fig. 3.1, Table 3.2). Slope averaged 20.9°, but was less than 10° in several large areas including Cades Cove, White Oak Sinks, and Sugarlands (Fig. 3.1, Table 3.1). Because it lay on the opposite side of the primary ridgeline from the NCSA, the aspects on the TNSA tended toward the north and west (Fig. 3.1, Table 3.3). Average habitat use probabilities were greater for males than females on this study area (Table 3.1). Male habitat use probabilities were highest in the eastern portion of the TNSA, whereas female habitat use probabilities were highest in the southern portion (Fig. 3.1).

Methods

Data Collection. Data were collected from 546 individual black bears captured 765 times from both study areas (Table 3.4). Personnel compiled 295 captures of 224 individual bears in the NCSA from 1994 to 1998 and 470 captures of 322 individual bears in the TNSA from 1989 to 1998. I coordinated the capture of black bears in the NCSA and TNSA from 1994 to 1997 and personally lead trapping efforts on the NCSA during this time period. Other personnel from the University of Tennessee subsequently collected data from both study areas in 1998. The TNSA consisted of 8 traplines with 6 – 9 trap sites each; traplines averaged 587 m between successive trapsites, and trapsites averaged 774 m in elevation (Table 2.2). The NCSA consisted of 8 traplines with 7 trapsites each; trapsites averaged 908 m in altitude and 694 m between them (on each line) (Table 2.2). Establishment of traplines and trapsites in the NCSA took several days in 1994 and resulted in less trapping effort that year than in subsequent years (Table 3.4). The NCSA traplines were placed to approximate the elevations and topographic positions of the TNSA traplines. All trapsites were positioned away from trails so that hikers could not easily see or hear captured bears.

Project personnel captured and handled bears by means of standard techniques (Johnson and Pelton 1980) every summer from May to August. Two crews on each study area trapped 2 traplines simultaneously for 15 days each. Then, after a 2 – 4 day hiatus, crews moved on to the next 2 traplines. This process resulted in 4 trapping periods each summer on each study area (Table 2.2). The standard trap type was a cubby set; however, trailsets, brush cubbies, trick sets, and double sets also were used.

Table 3.4. Trapping data from North Carolina and Tennessee black bear study areas in Great Smoky Mountains National Park, summers 1994 - 1998.

Year	Study Area[1]	Trapnights	Total Captures	Initial Captures	Within Year Recaptures	Previous Year Recaptures	Trapnights per Capture
1994	TNSA	783	66	63	3	0	11.9
	NCSA	431	27	27	0	0	16.0
1995	TNSA	784	98	73	8	17	8.0
	NCSA	780	60	52	5	3	13.0
1996	TNSA	791	82	54	5	23	9.6
	NCSA	777	63	49	6	8	12.3
1997	TNSA	793	135	79	16	40	5.9
	NCSA	776	89	59	6	24	8.7
1998	TNSA	780	89	53	9	27	8.8
	NCSA	732	56	37	2	17	13.1
Total	TNSA	3,931	470	322	41	107	8.4
	NCSA	3,496	295	224	19	52	11.9
Grand Total	Both	7,427	765	546	60	159	9.7

[1]TNSA = Tennessee study area; NCSA = North Carolina study area.

Personnel immobilized bears by injection of a 10:5:1 mixture of Ketaset (ketamine hydrochloride, Aveco Co., Inc., Fort Dodge Iowa), Rompun (xylazine hydrochloride, Rugby Laboratories, Inc., Rockville Center, New York), and Carbocaine-V (mepivicaine hydrochloride, Sterling Drug Inc., McPherson, Kansas) (KRC). Personnel administered KRC intramuscularly via jab pole syringe or blowpipe dart at 1 cc per 25 kg bear weight. Once immobilized, bears were treated with ophthalmic ointment to moisturize eyes and triple anitbiotic to disinfect minor cuts and wounds. Personnel subsequently measured, weighed, ear-tagged, and lip-tattoed all bears. Also, a premolar tooth was extracted for aging by use of cementum annuli (Willey 1974) and blood and hair samples were collected for future serological and genetic analyses unrelated to this project. Selected adult females and yearlings were fitted with radio collars (Telonics, Mesa, Ariz. and Ursus Technologies, Williamsburg, Virginia). In 1996, personnel placed colored ear streamers and 2" cotton collars on bears in both study areas for identification in remote camera resights to be collected later in the summer. Orange streamers and collars were used on the Tennessee study area whereas yellow streamers and collars were used on the North Carolina study area. In 1997 and 1998, personnel placed green or blue and orange colored ear streamers, respectively (without collars) on bears in the North Carolina study area only. Personnel revived bears by injection of Yohimbine (Lloyd Laboratories, Shenandoah, Iowa) and recorded all data on standard University of Tennessee bear capture forms.

To perform denwork, project personnel homed in on radio-collared females from March through May, 1994 to 1998. I coordinated these efforts for both study areas and

personally conducted all denwork on the NCSA during this time period. Once at the densite, personnel determined the type of den, immobilized the female if possible, handled cubs, recorded pertinent information, and withdrew before the female awoke from anesthesia. Personnel investigated tree dens with climbing ropes and ascending gear. Personnel used arrows or fishing weights to lift fishing line over suitable upper story branches and then pulled climbing rope over these branches. Climbers then ascended the rope and peered into tree cavities near the densite. Ground dens required no special effort or equipment and accounted for the majority of females that were immobilized.

Population Characteristics. I compared data on bear densities, sex ratios, ages, litter sizes, survival rates, and weights between the NCSA and TNSA. I used t-tests and chi-square analyses (SAS Institute, Inc. 1990) to check for significant differences, and employed a Bonferonni-type adjustment to the alpha levels to adjust for the multiple number (8) of tests performed. This adjustment lowered the alpha level for all tests from 0.05 to 0.00625.

Sex Ratio. I determined the sex ratio of bears captured on each study area from summer trapping data. I then compared the overall sex ratio between the study areas with a 2 x 2 Chi-square analysis. I tested the following null and research hypotheses:

H_0: Ratio of male and female bears did not differ significantly between the NCSA and TNSA.

H_R: Ratio of male and female bears did differ significantly between the NCSA and TNSA.

Age Distribution. I determined the age distribution of bears captured on each study area from teeth collected during summer trapping. Teeth were decalcified, sectioned longitudinally, mounted, stained, and aged according to techniques described by Willey (1974) and Matson et al. (1993). When discrepancies in age arose between multiple teeth from the same bear or when ages were questionable given the known history of a bear, I weighed all available information and derived the most appropriate age for the bear. Generally, I weighed ages from earlier teeth greater than ages from later teeth (from the same individual) because potential sources of aging errors increase with the age of the bear. I compared the overall age distribution for each sex between the study areas with a 2 x 12 Chi-square analysis. I excluded cubs and combined bears of ages 11.5 and greater into a single category due to small sample sizes. I tested the following null and research hypotheses on each sex:

H_0: Frequency of bear ages did not differ between the NCSA and TNSA.

H_R: Frequency of bear ages did differ between the NCSA and TNSA.

Body Size. I used weight as a surrogate for body size (assuming that larger bears had greater weight) and compared weights collected during summer trapping on each study area. I compared weights of all captured bears and weights for yearlings only. For these analyses, I used t-tests to test the following null and research hypotheses for each sex:

H_0: Weights did not differ between the 2 study areas.

H_R: Weights did differ between the 2 study areas.

Litter Size. I determined litter sizes of bears from winter denwork. Cubs were handled in dens where their mother could be immobilized. I compared overall litter sizes between the NCSA and TNSA with a T-test, and tested the following null and research hypotheses:

H_0: Litter size did not vary significantly between the 2 study areas.

H_R: Litter size did differ between the 2 study areas.

Survival. I used the Kaplin-Meyer staggered entry model (Pollock et.al. 1989) to estimate female survival rates from radio-collared bears. I did not estimate survival rates of males because male bears were not radiocollared during this study. I compared annual survival rates of females between the NCSA and TNSA with a t-test, and tested the following null and research hypotheses:

H_0: Female survival rates did not differ significantly between the 2 study areas.

H_R: Female survival rates did differ significantly between the 2 study areas.

Density. I compared density estimates for each model from 1994 – 1998 (see Chapter II) between the 2 study areas. I used t-test analyses to test the following null and research hypotheses:

H_0: Density estimates did not differ between the NCSA and TNSA.

H_R: Density estimates did differ between the NCSA and TNSA.

Results

Sex Ratio. More male than female bears were captured on each study area, with sex ratios (males:female) averaging 1.53:1 and 1.48:1 for the NCSA and TNSA, respectively (Table 3.5). The sex ratios fluctuated annually on each study area, reaching their greatest level (3.67:1) in 1996 on the NCSA and their smallest level (1.09:1) in 1997 on the TNSA. Sex ratios did not differ between the study areas (X^2=0.137, df=1, P = 0.711).

Age Distribution. Female bears averaged 5.99 and 6.23 years of age on the NCSA and TNSA, respectively (Table 3.6). Male bears averaged 4.59 and 4.25 years of age on the NCSA and TNSA, respectively (Table 3.6). The distribution of female bear ages was significantly different than that of male bears (X^2=59.823, df=10, P = 0.001), with females tending to be older than males (Fig. 3.2). Although there were differences in the percentage of bears in various year classes, the distribution of female and male bear ages did not differ significantly between the 2 study areas (females X^2=12.626, df=10, P = 0.245; males X^2=12.590, df=10, P = 0.247).

Body Size. Female bears averaged 42.5 kg on the NCSA and 43.0 kg on the TNSA (Table 3.7). Male bears averaged 65.0 kg on the NCSA and 65.9 kg on the TNSA (Table 3.7). Male bears were significantly larger than female bears (P = 0.0001). The weights of female and male black bears did not vary significantly between the 2 study areas (females P = 0.8017; males P = 0.7983). Yearlings averaged 27.8 kg (N = 21; Std.

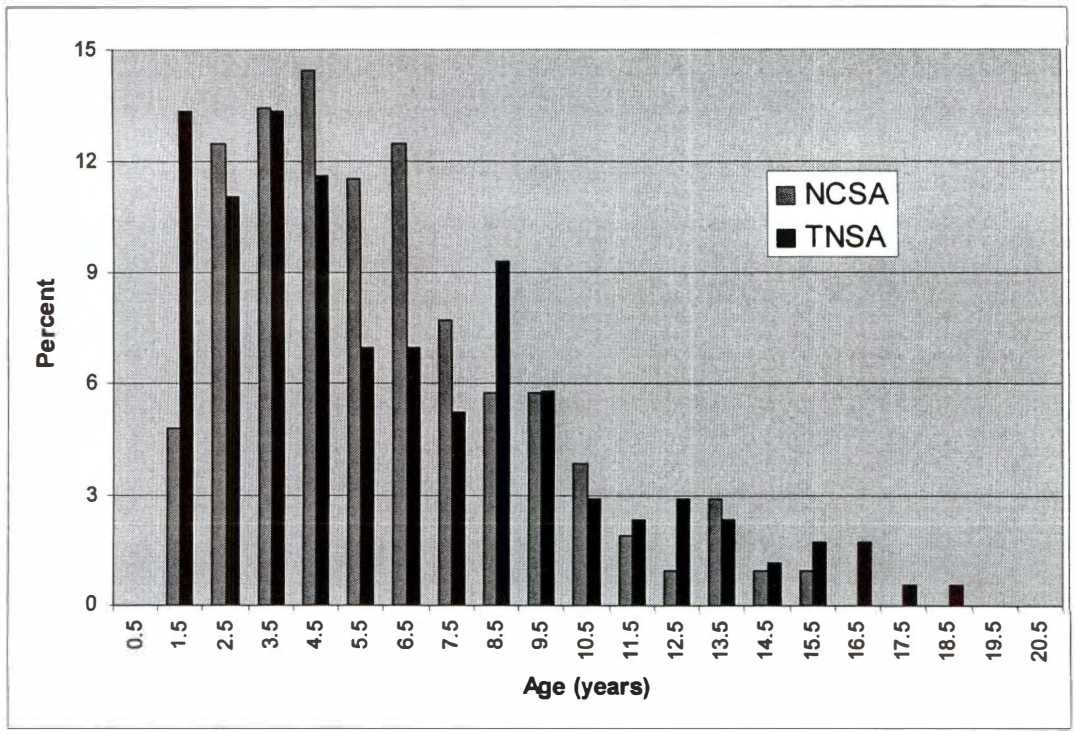
Table 3.5. Black bear sex ratios for North Carolina and Tennessee study areas in Great Smoky Mountains National Park, summers 1994 - 1998.

	North Carolina Study Area			Tennessee Study Area		
Year	♂	♀	♂:♀	♂	♀	♂:♀
1994	16	11	1.45:1	42	21	2.00:1
1995	30	23	1.30:1	49	40	1.23:1
1996	44	12	3.67:1	50	26	1.92:1
1997	44	38	1.16:1	60	55	1.09:1
1998	30	23	1.30:1	49	31	1.58:1
Total	164	107	1.53:1	394	267	1.48:1

Table 3.3. Black bear ages for North Carolina and Tennessee study areas in Great Smoky Mountains National Park, summers 1994 - 1998.

	Age (years)											
	North Carolina Study Area						Tennessee Study Area					
	Males			Females			Males			Females		
Year	N	Mean	STD	N	Mean	STD	N	Mean	STD	N	Mean	STD
1994	16	4.44	2.08	11	4.77	2.15	41	4.09	1.86	20	6.60	3.16
1995	30	3.93	1.79	22	5.41	2.81	40	4.30	2.69	46	6.54	4.43
1996	43	5.45	2.68	12	7.00	3.61	45	4.74	2.68	23	4.85	2.99
1997	44	4.16	2.46	36	6.17	3.30	57	4.04	2.61	53	6.18	4.50
1998	30	4.70	2.52	23	6.33	3.42	48	4.13	2.38	30	6.63	3.91
Total	163	4.59	2.43	104	5.99	3.17	231	4.25	2.46	172	6.23	4.06

A.



B.

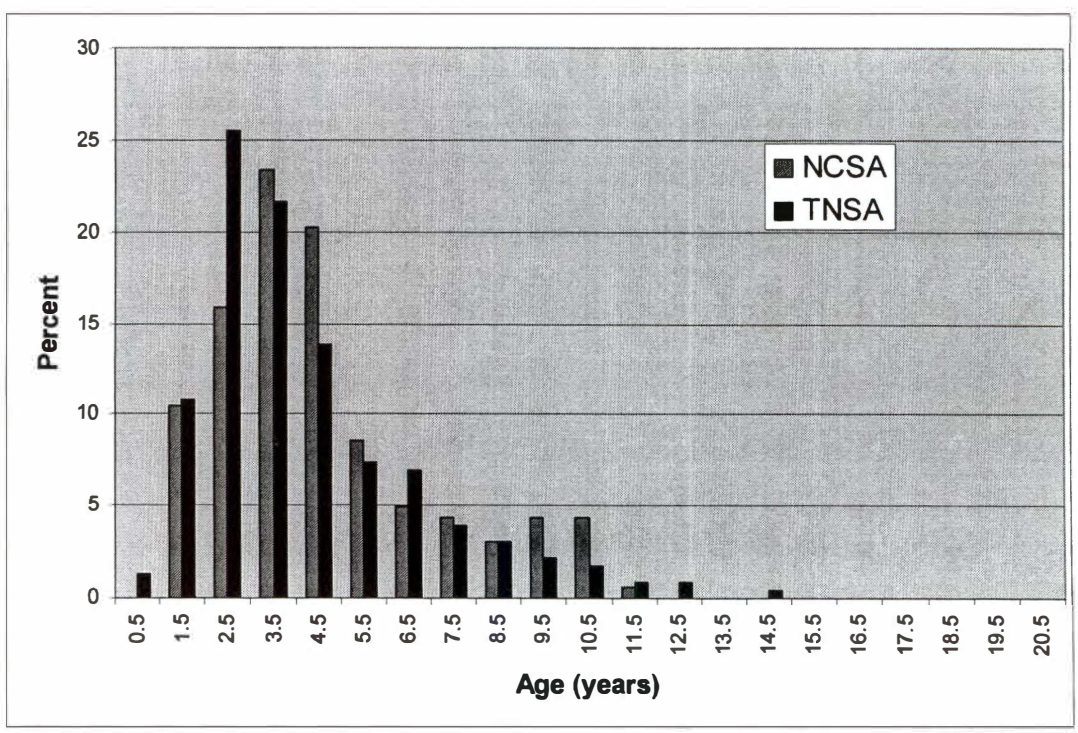


Figure 3.2. Age distributions of (A) female and (B) male black bears for North Carolina and Tennessee study areas in Great Smoky Mountains National Park, summers 1994 – 1998.

Table 3.7. Black bear weights for North Carolina and Tennessee study areas in Great Smoky Mountains National Park, summers 1994 - 1998.

	Weight (kg)											
	North Carolina Study Area						Tennessee Study Area					
	Males			Females			Males			Females		
Year	N	Mean	STD	N	Mean	STD	N	Mean	STD	N	Mean	STD
1994	15	73.9	25.3	11	47.2	16.8	41	70.4	33.7	21	48.0	10.7
1995	30	64.8	29.9	23	43.3	15.5	39	78.6	40.0	48	45.0	14.7
1996	30	60.0	27.2	11	49.1	14.9	46	65.9	41.1	24	34.3	13.9
1997	42	65.0	33.3	38	39.8	14.4	32	49.3	21.5	41	45.4	12.3
1998	28	65.5	34.0	20	40.5	12.3	36	61.7	33.1	25	39.3	10.8
Total	145	65.0	30.6	103	42.5	14.7	194	65.9	36.1	159	43.0	13.6

= 39.9) on the NCSA and 23.5 kg (N = 39; Std. = 17.1) on the TNSA. Yearling weights did not differ between the 2 study areas ($P = 0.2899$).

Litter Size. The number of females with cubs in dens peaked in 1994 (9) and 1996 (13) on both study areas. Six dens had cubs during all other years combined. The litter size of 8 dens on the NCSA averaged 2.1 cubs, whereas the litter size of 20 dens on the TNSA averaged 2.7 cubs (Table 3.8). The TNSA had more 3 and 4 cub litters than the NCSA, but overall litter sizes were not significantly different between the 2 study areas ($P = 0.0925$).

Survival. Four radio-collared females died on the NCSA and 8 radio-collared females died on the TNSA during 1994 – 1998. Two bears (50%) on the NCSA were legally harvested outside the Park, 1 bear (25%) died of natural causes, and 1 bear (25%) died of unknown causes. Five bears (63%) on the TNSA died of natural causes and 3 bears (37%) were legally harvested. The survival rate ranged from 0.600 to 1.000 on the NCSA and, when combined for all years, equaled 0.931 (Table 3.9). The survival rate ranged from 0.769 to 1.00 on the TNSA and, when combined for all years, equaled 0.905. Female survival rates did not differ between the 2 study areas ($P = 0.7985$).

Density. Lincoln-Petersen density estimates of black bears on the NCSA and TNSA averaged 1.63 and 1.77 bears/km^2, respectively (Table 2.9). Camera resight density estimates of black bears on the NCSA and TNSA averaged 0.79 and 0.65 bears/km^2, respectively (Table 2.9). Back dating density estimates of black bears on the NCSA and TNSA averaged 0.73 and 0.93 bears/km^2, respectively (Table 2.9). Jolly-Seber density estimates of black bears on the NCSA and TNSA averaged 0.94 and 1.20

Table 3.8. Black bear litter size for North Carolina and Tennessee study areas in Great Smoky Mountains National Park, summers 1994 - 1998.

	Total Number of Litters	
Litter Size	North Carolina Study Area	Tennessee Study Area
1	1	1
2	5	7
3	2	10
4	0	2
N	8	20
Average Litter Size	2.1	2.7

Table 3.9. Female black bear survival rates for North Carolina and Tennessee study areas in Great Smoky Mountains National Park, summers 1994 - 1998.

	North Carolina Study Area			Tennessee Study Area		
Year	N	Survival Rate	95% CI	N	Survival Rate	95% CI
1994	5	1.000	---	14	1.000	---
1995	15	1.000	---	26	0.885	0.769 – 1.000
1996	16	1.000	---	13	0.923	0.784 – 1.062
1997	17	0.882	0.739 – 1.026	19	0.790	0.627 – 0.952
1998	5	0.600	0.267 – 0.933	12	1.000	---
Combined	58	0.931	0.868 – 0.994	84	0.905	0.845 – 0.965

bears/km^2, respectively (Table 2.9). Density estimates did not differ between study areas for the Lincoln-Petersen, Bailey's binomial, or Jolly-Seber models ($P = 0.6410$, 0.6607, and 0.5702, respectively). Density estimates generated from the back dating model differed between study areas ($P = 0.0021$).

Discussion

Bears within the NCSA and TNSA exhibited similar population characteristics that fell within the range normally reported for black bears, particularly those in the southern Appalachian Mountains. The 60/40 sex ratio split between males and females was expected because of the larger home range size of males, which brought them into contact with traps more often than females. For this reason, I did not conclude that the population as a whole had a biased sex ratio, rather that this finding was an artifact of trap heterogeneity between males and females. The sex ratios documented in this study were similar to those found by Beeman (1975), Pelton and Beeman (1975), and McLean (1991). Sex ratios did fluctuate from year to year, with larger proportions of males corresponding to years of high cub production (1994 and 1996). I hypothesize that this finding relates to females with cubs traveling over smaller areas and therefore coming into contact with trap sites less often than in years with yearlings or no young. If correct, this phenomenon could be used to track relative proportion of females with cubs, and indicated that reproduction was synchronized within the Park during 1994, 1995, and 1996. Less extreme sex ratios during 1997 and 1998, therefore, may have indicated a breakdown of synchronicity among breeding females.

The significantly older age distribution of females compared to males was expected. Males travel over larger distances, which brings them into contact with potential sources of mortality (e.g., roadkill and legal harvest) at higher rates than females. Also, subadult males tend to disperse more than females and must compete with other males to find adequate nutrition and mates. Conversely, females tend to inherit a portion of their mother's range and do not tend to travel over great distances or directly compete for mates (Alt 1978, Rogers 1987a, 1987b, Schwartz and Franzmann 1992). I attributed the lack of cubs and yearlings in the age distributions to trap heterogeneity and not to lack of recruitment. Additionally, errors inherent in the aging process made it difficult to assign all bears to year classes and may have contributed to some of the unevenness in the age distributions, particularly for the longer-lived females. Overall, the high average age for both sexes in conjunction with the presence of older bears was consistent with high survival estimates that suggested a population exploited only marginally to lightly (Bunnell and Tait 1981).

The average weights of bears, including yearlings, which would be expected to vary most in accordance with nutrition, on each study area were remarkable only in their similarity. Changes in the proportion of subadults and adults in the trapping sample may explain the fluctuation in average weights from year to year for each sex on both study areas. Alternatively, weights may have fluctuated with changes in food availability and nutrition. Although I was unable to find clear patterns, most likely both factors combined to affect the weights and body sizes of captured bears. My analysis of weights indicated that habitat differences, if present, were not of sufficient magnitude to dramatically

increase the size of bears on either study as compared to the other. As expected and demonstrated in numerous other studies, males were significantly larger than females (Bunnell and Tait 1981, Eason 1995).

Average litter sizes on both study areas fell within reported ranges for black bears in the southern Appalachians (see McLean 1991, Garshelis 1994). Average litter size for the TNSA (2.7) was higher than the 2.0 cubs/litter reported by McLean (1991), but comparable to values reported by Wathen and Pelton (1984) (2.6) and Eiler et al. (1989) (2.58). Average litter size for the NCSA (2.1) was comparable to McLean's (1991) value, but lower than those reported by Wathen and Pelton (1984) and Eiler et al. (1989). The combined average litter size between both study areas (2.5), like the value for the TNSA, closely matched reported values by Wathen and Pelton (1984) and Eiler et al. (1989), but were higher than that reported by McLean (1991). Denwork was difficult to complete on family groups because of the remoteness of den sites, particularly on the NCSA, and propensity for females with cubs to den high up in old, large trees. Therefore, sample sizes were limited, which most likely accounted for the differences in average litter size among the various studies.

Based on the number of females documented with cubs each winter (9 in 1994, 3 in 1995, 13 in 1996, 3 in 1997, and 0 in 1998), bears in GSMNP seemed to be in breeding synchrony, with most females producing cubs in 1994 and 1996. This synchrony coincided with a marked hard and soft mast failure during 1992, which seemed to have prevented females from raising cubs in 1993. Another mast failure in 1997 preempted cub production in 1998, which should have been high. These findings indicated that

reproduction in GSMNP was sensitive to fall food shortages, which when they occurred, caused most females to bear young in the same year as opposed to normal conditions when half of them would be reproducing each year. Consequences of this pulse phenomenon include increased competition among large cohorts every other year, fluctuations in dispersal and mortality (particularly legal harvest as young bears search for living space), and large changes in population abundance and density from year to year.

Along with sound reproductive output, female survival was high, indicating a healthy population of bears in GSMNP. Because the long-term protocol for research in the Park restricted radiocollar placement to females only, I was unable to calculate male survival. In an attempt to quantify this parameter, I performed Jolly/Seber analyses for males and females separately on the TNSA study area from 1989 – 1998, where sample sizes were larger than for the NCSA. Sample sizes were limited, so these survival estimates should be interpreted with caution. Models A and B were identified as the best fitting models; however, model A yielded estimates above 1.00 for several years, so I disregarded it. Using model B, which assumed equal survival per unit time, female survival equaled 0.87 with a 95% confidence interval of 0.81 – 0.93 and male survival equaled 0.64 with a 95% confidence interval of 0.56 – 0.71. These estimates seemed reasonable given the comparability of the female survival rate with those calculated from radio-collared females. If accurate, these estimates indicate that male bears suffer a much higher mortality/emigration rate than females, probably because of their increased movements. These results also would explain the younger age distribution of males documented in this study. The Jolly-Seber estimate may be an under-representation of

actual male survival, possibly due to small sample sizes and difficulty in recapturing male bears. More likely, because the Jolly/Seber model does not distinguish between mortality and emigration, these results may indicate significant levels of male movement out of the study area. Overall, female mortality rates were easily sustainable, whereas male survival rates, if accurate, were severe (Bunnell and Tait 1981), which was not supported by the sex ratio and age distribution data, again indicating that emigration was likely occurring.

The only population characteristic that differed between the 2 study areas was density, as estimated by back dating; estimates from the other models did not vary between study areas, even though they tended to be higher on the TNSA. Comparison of densities between the study areas was hampered by extremely small sample sizes; therefore, I emphasized the back dating estimates, which were generated for every year. Density estimates from the back dating model on each study area mirrored each other in trend, with the NCSA density consistently about 25% lower than that of the TNSA (Fig. 3.3). Some obvious possible explanations for the difference in density can be discounted based on other data collected in this study. Female rates of survival were alike on each study area, indicating that mortality was not driving the difference, unless it occurred differentially for males or cubs and yearlings. Additionally, the similarity in sex ratios and age distributions between the areas suggested that no pronounced demographic factors accounted for the difference. I did not detect any evidence of poaching at any level on either study area, therefore eliminating that factor as a significant impact. Cub production may have been higher on the TNSA, but not at a statistically significant level. Small sample size from the NCSA precluded a robust comparison, but also most likely

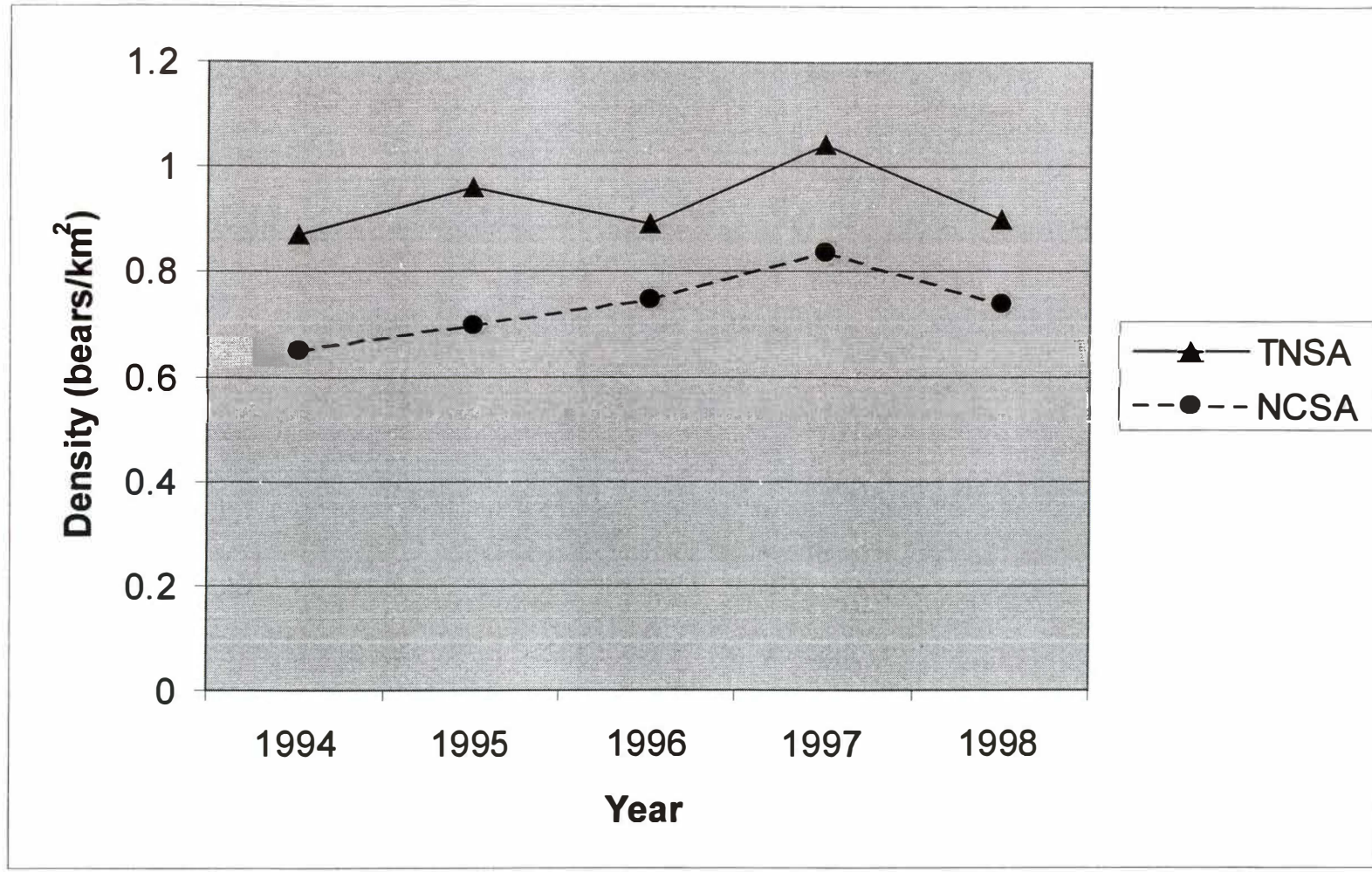


Figure 3.3. Black bear density estimates (bears/km^2) from the back dating model for North Carolina (NCSA) and Tennessee (TNSA) study areas in Great Smoky Mountains National Park, summers 1994 - 1998.

accounted for the difference in average litter size. However, if even a slight difference in cub production exists, it would provide higher recruitment on the TNSA than the NCSA. Even so, some other difference between the areas would be necessary to hold a higher density of bears on the TNSA.

Another possibility was that the population estimates were biased between the 2 study areas. I concluded that this was unlikely given the use of consistent methodology and comparison of identical time frames between the TNSA and NCSA. The backdating model was the only one that provided estimates for every year on both study areas, and was significantly correlated with yearly trapping results. Consequently, there was potential for factors affecting trap success to influence the density trends. Identical baits and trapping methodologies were used on each study area, so they should have had negligible affect. Differences in trap placement could have affected trap success. Traplines and trapsites on the TNSA had evolved over 25+ years of research prior to initiation of this study and likely were located in ideal areas. Traplines and trapsites on the NCSA were placed during 1994 and did not change throughout the course of the study. Errors in effective study area delineation, as determined by buffering trapsites with a fixed radius, tended to affect the TNSA slightly more than the NCSA, (Table 2.10). The above factors would tend to result in increased density on the TNSA compared to the NCSA; however, for the reasons stated, I believe that if present, these differences were marginal.

Elimination of the above factors left only one evident alternative to explain the differences in density between the 2 study areas – habitat quality. Although not drastic in

most regards, there were several clear differences between the NCSA and TNSA. The physical factors that drove these differences were aspect, elevation, and slope. The NCSA fell on the southern side of the main ridgeline dividing North Carolina from Tennessee and consequently had predominantly south-facing slopes (Table 3.4). Conversely, the TNSA fell on the north side of the state line and had predominantly north-facing slopes (Table 3.3). Elevations tended to be higher on the NCSA than the TNSA, with significant portions high enough to harbor northern hardwood and spruce-fir forests (Tables 3.1 and 3.2). The NCSA had, on average, steeper slopes than the TNSA, which also had large relatively flat areas such as Cades Cove and Spruce Flats (Table 3.1). The NCSA had no comparably large flat areas, but did have Fontana Lake to its south. The TNSA had no large bodies of water in or adjacent to it.

The result of these differences was contrasting portions of forest cover types within each study area. Cove hardwood, mesic oak, and mixed mesic hardwood forests made up large portions of the NCSA, whereas xeric oak, tulip poplar, and pine dominated the TNSA (Table 3.2). Overall, these differences in cover types resulted in a 12.4% greater white oak crown volume on the TNSA and a 17.1% greater red oak crown volume on the NCSA (Inman 1997). Shrub coverage of soft mast producing species was similar on both study areas (Inman 1997). Based on these results, I concluded that white oak prevalence had a disproportionately large affect on density as compared to red oak prevalence. This finding was supported by the fact that white oak acorns contain less tanins than red oak acorns and, thus, tend to be more palatable to wildlife species. Additionally, van Manen et al. (in press) found that white oak mast production correlated

strongly with bear abundance estimates in GSMNP; they found no such relationship with red oak mast production.

In addition to the differences in vegetation between the study areas, habitat use probabilities also varied. Female habitat use probabilities tended to be slightly higher on the NCSA and male habitat use probabilities tended to be substantially higher on the TNSA, but overall combined habitat use probabilities were 8.4% higher on the TNSA than the NCSA (Table 3.1). Differences in habitat use between sexes was attributed to males tending to respond to slightly different factors (vegetation type, elevation, and proximity to roads) than females (disturbance history, elevation, and proximity to human activity sites) (van Manen 1994). Because males may exclude females from areas of high habiatat quality (van Manen 1994), male habitat use values may more accurately represent habitat quality than female habitat use values. The lack of difference in sex ratios between the study areas that I found in this study indicated that differences in habitat use probabilities by gender did not translate into significant differences in numbers of males and females on each study area. Consequently, I hypothesized that the overall higher habitat use probabilities on the TNSA (indicating preferred habitats) combined with the high white oak production (indicating higher food quality) on the TNSA accounted for the significant differences in density between the TNSA and NCSA.

Black bears in GSMNP, particularly females, had relatively small home ranges and movements compared to other black bear populations across North America (van Manen 1994) (Appendix B). Bears rarely crossed from one trapline to another, much less across study areas. During this 5-year study, 765 captures resulted in only 3 cross-study

area movements by male bears; no females were detected making such movements. This tendency for limited movements coupled with the similarities in population characteristics across the 2 study areas and apparent response to habitat quality (particularly fall mast production (Garshelis and Pelton 1981)) resulted in consistent and predictable density trends through time. High survival rates and regular cub production led to increasing densities of bears on both study areas during years of adequate mast production. Then, following major mast failures (usually fall hard mast), fall movements increased exponentially and mortality rates spiked dramatically (Fig. 3.4), leading to population mixing and sharp declines in density. During such "fall shuffles" (Reynolds and Beecham 1976, Garshelis and Pelton 1981, Carr 1983, Garris 1983, and Hellgren and Vaughan 1990), it was not uncommon for Park bears to be harvested several counties away from GSMNP, with some turning up as far away as northern Georgia and western South Carolina. Because mortality generally was skewed toward younger bears, it seemed that dominant bears remained in the Park, forcing smaller, less dominant bears out in search of food. Even with these sometimes-extensive movements of individuals, most seemed to return to their normal home ranges because few bears crossed between study areas in different years. The breeding synchrony that followed mast failures produced marked pulses of cubs that quickly drove densities back up from post mast failure levels. These trends were clearly evident in the mortality (Fig. 3.4), cub production (Table 3.8), and density estimate data (Figs. 2.4, 2.5. and 3.3) in GSMNP during 1992 and 1997, years of the 2 most recent severe mast failures.

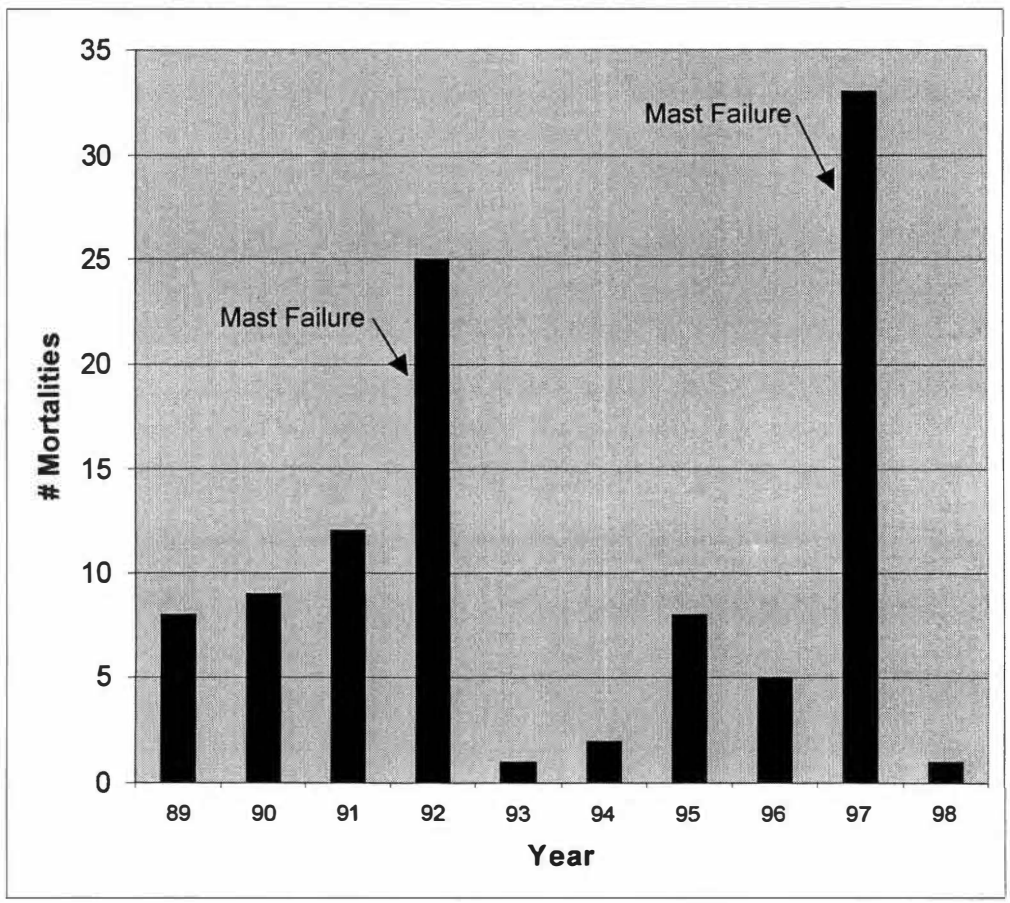


Figure 3.4. Reported mortalities of tagged black bears with years of mast failure identified in Great Smoky Mountains National Park, summers 1989 – 1998.

The population characteristics documented in this study indicated that, although black bears in the 2 study areas exhibited similar sex ratios, age distributions, litter sizes, female survival, and weights, their densities varied significantly. No evidence of poaching or other mortality factors was found to account for differences in density. Instead, habitat characteristics were most likely the cause. Bears in GSMNP seemed to respond to higher habitat quality by increasing density, with severe mast failures affecting bears proportionally on each study area. The implications of such dynamics include long-term unpredictability of major mortality events and potential for density of bears to increase significantly during long periods of adequate nutrition. These effects result in years of mortality spikes, usually in the form of legal harvest, which may be misinterpreted by land managers and the public as indicative of a population crash. Such crashes did not materialize during the course of this study; instead the populations quickly rebounded because of prolific cub production produced from breeding synchrony that was induced by severe mast shortages followed by years of adequate nutrition. Through the sheer number of bears in the Park, the latter effect may result in increased human/bear interactions and conflicts during consecutive years of adequate food supply. Park managers should be aware of this tendency toward high density and take appropriate precautions with visitors. The findings of this study indicated that density-dependent regulatory factors were not operating at noticeable levels at the range of densities encountered during this study (Garshelis 1994); instead population levels seemed to be governed by major density-independent system perturbations in the form of mast failures.

CHAPTER IV

DISPERSAL

Introduction

Although black bears can travel hundreds of kilometers, many remain near their place of birth. Several studies have documented the extensive dispersal distances of bears (Alt 1978, Beeman 1975, Garshelis 1978, Quigley 1982, Carr 1983), but only a few have conducted research on black bear dispersal within a single population (Rogers 1987*a*, 1987*b*; Schwartz and Franzmann 1992). In GSMNP and surrounding national forests, only Clevenger and Pelton (1990) investigated the dispersal of juvenile black bears. They found that family units separated in mid-June and that some reassociations occurred. However, because of small sample sizes and short duration of the study, they did not document when final dispersal occurred and how far dispersing bears traveled.

Based on anecdotal observations and the above studies, researchers have described the typical dispersal of juvenile black bears as following a predictable sequence of events. Cubs are born in the den, spend their first year with their mother, and then den with her again (Rogers 1987*a*, 1987*b*; Reynolds and Beecham 1980). When they emerge from the den during their second year, they gradually become independent from their mother and begin to stray farther from her (Rogers 1987*a*, Reynolds and Beecham 1980). This time of separation generally coincides with the summer breeding season and may serve to protect juveniles from aggressive dominant males attempting to breed with

estrous females. Upon separation from their mother, female and male juveniles are thought to take different paths. Female yearlings generally stay close to their mother and may inherit a portion of her home range (Alt 1978, Rogers 1987*a*), whereas male yearlings generally leave their natal areas and may be forced great distances away by dominant males that do not tolerate subdominant male bears in their territory (Alt 1978, Rogers 1987*b*, Schwartz and Franzmann 1992).

The consequences of this dispersal behavior may be profound. If female black bears do not disperse far from their natal areas, then recolonization of distant vacated range will be unlikely and slow (Alt 1978). Repatriation efforts that move females into unoccupied range may be necessary to augment natural dispersal and colonization (Smith and Clark 1994). Also, mortality rates of dispersing male black bears may be greater than those of young females that do not disperse (Alt 1978, Schwartz and Franzmann 1992). These males likely will constitute a large proportion of roadkills and hunter harvest in areas peripheral to core bear populations. Additionally, Rogers (1987*b*) hypothesized that young males in high-density populations may delay dispersal until they obtain sufficiently large body mass to compete with dominant males in the population. Such behavior would lead to dispersal dynamics contrary to the accepted pattern outlined above.

Understanding why some individuals disperse and others do not provides insight into gene flow between populations, range expansion capabilities, population regulation, and hunter harvest dynamics. Given the importance of dispersal for black bears, especially regarding hunter harvest in areas adjacent to sanctuaries like GSMNP, it is unfortunate that the technical constraints of conducting this type of research have

prevented investigative efforts in this area. This lack of information, coupled with the importance of understanding such a basic life history trait, make it important for researchers to learn more about black bear dispersal in GSMNP. The specific objectives of this study were to determine the timing of dispersal and demographic characteristics of dispersing individuals.

Study Area

Specific study areas were located within 2 portions of GSMNP, the North Carolina study area (NCSA) and the Tennessee study area (TNSA). Combined these study areas comprised over 35% of the total land area of GSMNP and were placed to represent the wide array of cover types occupied by bears within the Park. The NCSA was established in summer, 1994 and was active for 5 years, through summer, 1998. This study area totaled 400 km^2 and consisted of 8 traplines that stretched eastward from the southwestern boundary of GSMNP to highway 441 and southward from the North Carolina-Tennessee border to Fontana Lake. The TNSA was originally established in 1968 and has been continuously sampled, in various forms, to the present. Because of differing objectives for the studies that have been conducted on the TNSA, the specific study areas, traplines, and trapsites have changed slightly throughout the years. The general location for all of these studies has been the area stretching eastward from the northwestern boundary of GSMNP to highway 441 and northward from the North Carolina-Tennessee border to the northern boundary of the Park. During the last 10 years, the TNSA totaled 358 km^2.

Methods

I followed the usage of Shields (1987) and defined dispersal as "the movement of an organism from its site of origin to its first subsequent breeding site." I investigated the dispersal patterns of black bears in GSMNP with 2 techniques. In the first technique, I fitted selected yearlings with expandable radiocollars (Ursus Technologies, Williamsburg, VA) and tracked their movements from a fixed-wing aircraft every other week or as often as possible given weather and logistical constraints. I approached females known to have had cubs the previous year during winter denning (January through April) and attempted to immobilize the family group. Because of the propensity for females with yearlings to move when approached, I only was able to radiocollar 1 family group of 2 yearlings with their mother. Consequently, to enhance sample sizes, I had project personnel radio-collar 8 additional yearling bears captured during summer trapping. We assumed that bears weighing < 22.5 kg were yearlings, although 1 27 kg bear also was radio-collared as a yearling. I later verified their yearling status from ages estimated from analysis of cementum annuli in extracted teeth.

In the second technique, I calculated distance traveled between recaptures of individual bears. I used trapping data from summers 1968 to 1998 on the TNSA and 1994 to 1998 on the NCSA. I mapped the locations of initial and subsequent captures of individuals and calculated 590 (318 male and 272 female) straight-line distances traveled. Because the data were not distributed normally ($p = 0.0001$), I used the nonparametric Kruskal-Wallis test (SAS Institute, Inc. 1990) to check for significant differences among distances traveled by bears in different age classes and sexes. I employed a Bonferonni-type adjustment to the alpha levels to adjust for the multiple number of tests being

performed. This adjustment lowered the alpha level for all tests from 0.05 to 0.0055. I defined 3 age classes: yearlings (age = 1.5 years), subadults (age = 2.5 – 3.5 years), and adults (age = 4.5+ years), and grouped recaptures that occurred between age classes into 2 additional categories, yearling-subadult and subadult-adult. I did not analyze recaptures for cubs because of limited sample size (n = 2). No recaptures occurred between the yearling and adult age classes (most likely because of relatively small sample sizes (n = 48) and overall high trap success). Lastly, I documented and compared the age classes of all bears that traveled greater than an average home range diameter between recaptures (females = 2,600 m; males = 7,500 m) (van Manen 1994).

Results

Telemetry. Based on cementum annuli aging, 7 out of 10 bears radiocollared because they were thought to be yearlings (weight < 22.5 kg) actually were. Four of the yearlings were females and 3 were males. Dispersal distances among 6 of the yearlings were minimal, but two males exhibited significant movements from their original points of capture (Figure 4.1). The following accounts of individual yearlings provide details related to each.

Yearling 1315. Project personnel initially captured this male bear on 14 June 1996 on Rabbit Creek Trail. He weighed 30 kg and was the only bear radiocollared as a yearling even though he weighed > 22.5 kg. Project personnel captured him again on 22 June 1996 on the same trail. I monitored his movements until 17 November 1997 when I lost contact with him. He stayed in the vicinity of his capture location until 21 July 1997 when his signal was acquired somewhere up Eagle Creek, approximately 13 km to the

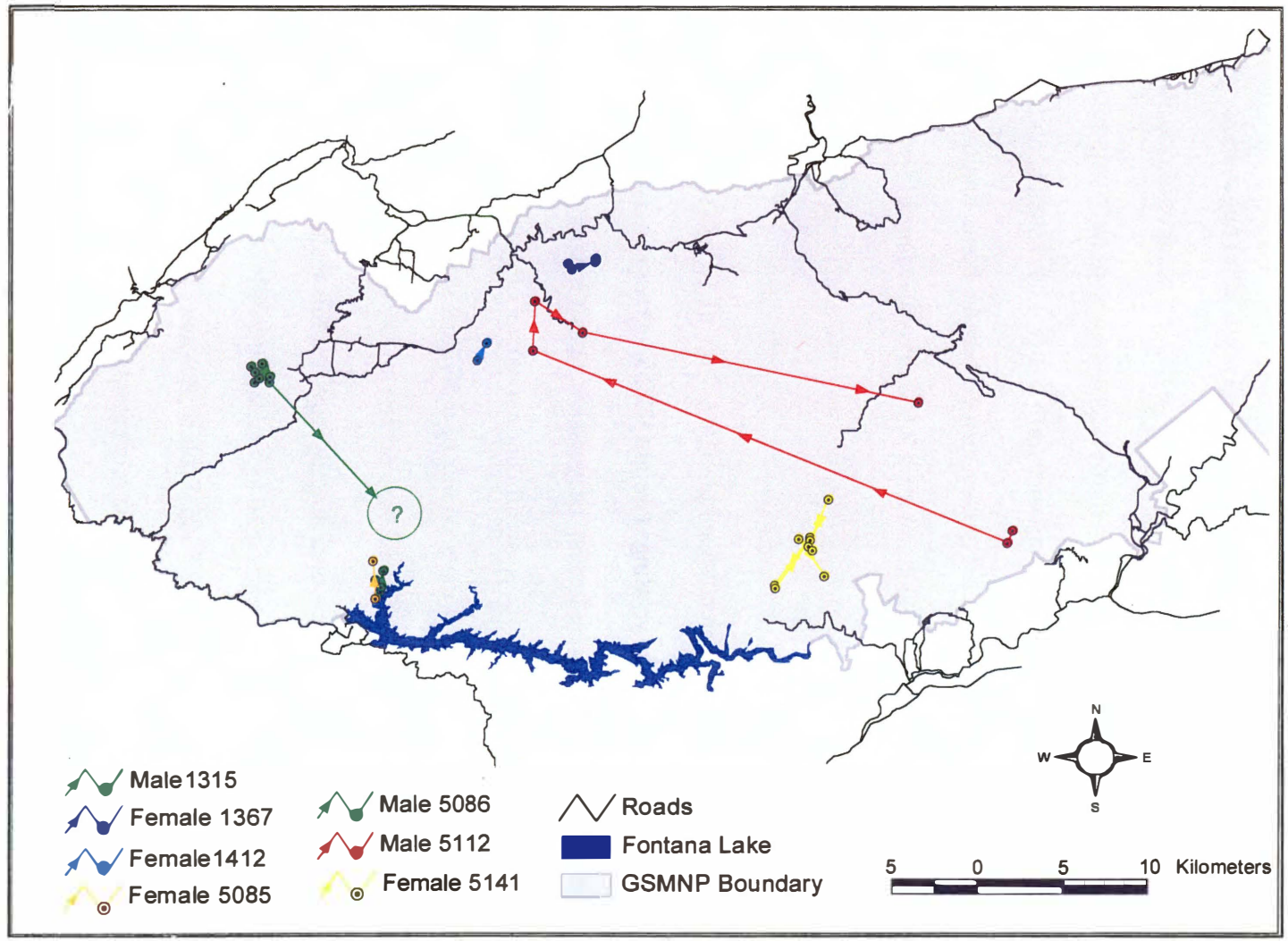


Figure 4.1. Movements of radiocollared yearling black bears in Great Smoky Mountains National Park, 1996 - 1998.

southeast. I was never able to precisely locate him after he left the Rabbit Creek Trail area because of weather and flight difficulties. The average distance among the 7 locations I plotted on him was 835 m (n=21, st. dev.=308 m, range 381–1,429 m). Although I was unable to document his movements as a 2.5-year old precisely, they indicated that he had moved and stayed approximately 13 km from his range as a yearling.

Yearling 1367. Project personnel captured this female bear on 9 June 1997 on Lumber Ridge Trail. She weighed 14 kg. I monitored her movements until 13 March 1998 when I lost contact with her. She stayed in the vicinity of her capture the entire time. The average distance among the 4 locations that I plotted on her was 1,159 m (n=6, st. dev.=672 m, range=180-1,664 m). I located her one additional time in the same area without plotting a precise location. She was later caught on Lumber Ridge Trail during summer 2000 in the same area (F. van Manen, University of Tennessee, personal communication)

Yearling 1412. Project personnel captured this female on 8 July 1997 on Bote Mountain Trail. She weighed 15 kg. I monitored her movements until 21 July 1997 (only 13 days) when I lost contact with her. She moved 1,172 m from her point of capture.

Yearling 5085. I captured this female bear on 18 February 1996 in the den on Shuckstack Mountain with her mother (5008) and male sibling (5086). She was part of the only family group radio-collared together during this study. She weighed 15 kg. After den emergence, she dropped her radiocollar, which was recovered 2,302 m away from the den on 2 April 1996.

Yearling 5086. I captured this male bear on 18 February 1996 in the den on Shuckstack Mountian with his mother (5008) and female sibling (5085). He was part of the only family group radio-collared together during this study. He weighed 23 kg. I monitored his movements until 20 September 1996 when I recovered his dropped collar. He stayed in the vicinity of Shuckstack Mountain and was captured by project personnel on 2 June 1996 on Lakeshore Dam Trail. The average distance among the 5 locations that I plotted on him was 896 m (n=10, st. dev.=439 m, range=295-1,775m).

Yearling 5112. Project personnel initially captured this male bear on 2 July 1996 on Deeplow Gap Trail. Project personnel subsequently captured him again on 8 July 1996 at the same trapsite. He weighed 23 kg. I monitored his movements until 21 January 1997 when I lost contact with him. He stayed in the Deeplow Gap area until 12 November 1996 when I located him on Defeat Ridge approximately 30 km away to the northwest. Yearling 5112 kept moving and circled back toward his point of capture, from which his last location was approximately 10 km away. The average distance among the 7 locations I plotted on him was 17,763 m (n=21, st. dev.=12,394 m, range=0-31,247 m).

Yearling 5141. Project personnel captured this female bear on 2 August 1996 on Springhouse Branch Trail. She weighed 14 kg. I monitored her movements until 13 March 1998 when I lost contact with her. She stayed in the Springhouse Branch/Forney Ridge area, where project personnel visited her in winter 1996-1997 den. The average distance among the 9 locations that I plotted on her was 2,464 m (n=36, st. dev.=1,542 m, range=161-6,261 m).

Recapture Distances. Recapture distances of bears varied significantly among age classes (X^2 = 26.7, df = 4, P = 0.0001) and between sexes (X^2 = 31.0, df = 1, P =

0.0001). Bears in the subadult and subadult-adult age classes exhibited the greatest distance among recaptures ($\bar{x}$ = 2,642 and 1,654 m, respectively), whereas yearlings exhibited the smallest distance ($\bar{x}$ = 328 m) (Table 4.1). Male bears moved greater distances among recaptures ($\bar{x}$ = 1,807 m) than did females ($\bar{x}$ = 811 m) (Table 4.1). Recapture distances of male bears varied significantly among age classes (X^2 = 18.7, df = 4, P = 0.0009), with subadult, subadult-adult, and adult age classes exhibiting greater distances among recaptures ($\bar{x}$ = 3,139, 1,924, and 1,441 m, respectively) than yearling and yearling-subadult age classes ($\bar{x}$ = 291 and 1,023 m, respectively) (Table 4.1). Adult and subadult-adult males traveled significantly farther among recaptures ($\bar{x}$ = 1,441 and 1,924 m, respectively) than did adult and subadult-adult females ($\bar{x}$ = 607 and 1,201 m, respectively) (X^2 = 25.2, df = 1, P = 0.0001 adults; X^2 = 7.7, df = 1, P = 0.0054 subadult-adults) (Table 4.1). Recapture distances did not vary significantly among age classes of females (range $\bar{x}$ = 494 – 1,523 m) (X^2 = 13.5, df = 4, P = 0.0091) or between sexes of yearlings ($\bar{x}$ = 494 and 291 m for females and males, respectively) (X^2 = 0.5, df = 1, P = 0.4775), yearlings-subadults ($\bar{x}$ = 1,523 and 1,023 m for females and males, respectively) (X^2 = 2.8, df = 1, P = 0.0929), and subadults ($\bar{x}$ = 995 and 3,139 m for females and males, respectively) (X^2 = 0.1, df = 1, P = 0.8035). Recapture distances for 6 females and 12 males were greater than the average home range diameter of each sex (Table 4.2). Females who exhibited these lengthy movements tended to do so as adults, whereas males tended to do so as subadults (Table 4.2).

Table 4.1. Recapture distances among age classes and sexes of black bears in Great Smoky Mountains National Park, 1968 – 1998.

	Recapture Distance (m)								
	Females[NS]			Males[S]			Males + Females[S]		
Age Class	N	Mean	Std. Dev.	N	Mean	Std. Dev.	N	Mean	Std. Dev.
Yearling[NS]	2	494	73	9	291	237	11	328	228
Yearling – Subadult[NS]	20	1,523	3,020	17	1,023	2,110	37	1,293	2,618
Subadult[NS]	16	995	594	53	3,139	6,008	69	2,642	5,339
Subadult – Adult[S]	52	1,201	2,438	87	1,924	2,595	139	1,654	2,552
Adult[S]	179	607	660	151	1,441	1,715	330	989	1,323
All[S]	272	811	1,470	318	1,807	3,136	590	1,348	2,556

[NS]Recapture distances did not differ significantly within class.
[S]Recapture distances differed significantly within class.

Table 4.2. Distance, age, and age class of bears that traveled farther than an average home range diameter between recaptures in Great Smoky Mountains National Park, 1968 - 1998.

Bear ID	Distance (m)	Age 1[1]	Age 2[2]	Age Class
Females:				
5017	2,913	3.5	5.5	Subadult – Adult
797	3,005	7.5	9.5	Adult
5102	4,088	10.5	12.5	Adult
620	9,525	2.5	11.5	Subadult – Adult
5175	14,102	1.5	2.5	Yearling – Subadult
744	15,445	3.5	7.5	Subadult – Adult
Males:				
5177	7,603	8.5	9.5	Adult
1426	7,630	2.5	2.5	Subadult
5176	8,850	1.5	3.5	Yearling – Subadult
5172	9,253	3.5	3.5	Subadult
5099	10,779	4.5	4.5	Adult
5183	14,797	3.5	5.5	Subadult – Adult
900	14,822	3.5	3.5	Subadult
5183	15,229	3.5	4.5	Subadult – Adult
1417	15,855	0.5	2.5	Cub – Subadult
1520	21,998	2.5	3.5	Subadult
5068	25,958	3.5	3.5	Subadult
5068	26,434	3.5	3.5	Subadult

[1]Age at first capture.
[2]Age at subsequent capture.

Discussion

The telemetry and recapture distance data indicated that bears in Great Smoky Mountains National Park conformed to dispersal patterns previously documented by Alt (1978), Rogers (1978 *a*, 1978*b*), and Schwartz and Franzmann (1992). Males tended to disperse farther and more often than females. Also, I found little evidence to suggest that black bears in Great Smoky Mountains National Park disperse as yearlings. Two radiocollared yearlings exhibited significant movements, but these travels occurred in the fall and most likely were associated with food-related movements that are common to bears in the southern Appalachians (Beeman and Pelton 1980, Carr 1983, Garris 1983, Garshelis and Pelton 1981, Quigley 1982, Villarrubia 1982). The other 5 yearlings stayed close to their points of capture, with only one moving farther than the diameter of an average home range for bears in the Park. Additionally, distances among recaptures of yearlings were the smallest of any age group investigated, averaging only 328 m.

Subadults moved the greatest distances among recaptures, indicating that dispersal may occur during this age interval (2.5 – 3.5 years old). Although not statistically significant after making the Bonferonni-type adjustment for multiple tests, male subadults tended to move greater distances among recaptures (average = 3,139 m) than did female subadults (average = 995 m). The tremendous variation in recapture distances among subadult males (std. dev. = 6,008) accounted for the lack of statistical significance and, coupled with the highly tailed distribution of distances, suggested that a few males tended to disperse long distances whereas most stayed close to their natal areas. Additionally, 10 of 12 males that moved greater than an average home range diameter between recaptures did so while in the subadult age class at some point during

the movement. Such delayed dispersal corresponded with findings by Schwartz and Franzmann (1992) and Rogers (1978*a*, 1978*b*). Rogers suggested that yearling males might delay dispersal until greater body size is reached to increase competitive advantage with other males in dense bear populations. Given the high density of bears documented in the Park (see chapter 1), the findings of this study are consistent with Rogers' hypothesis.

Given that most bears in Great Smoky Mountains National Park tended to disperse only a short distance from their natal areas, expansion of this population into adjacent unoccupied habitats should be slow. Additionally, if these habitats are separated from the Park by even relatively short distances, female bears will not reach them. This lack of dispersal suggests that population levels will tend to build up in the Park with males only occasionally dispersing out of occupied areas. Consequently, mortalities that occur outside the Park should tend to be subadult males, and densities within the Park may become high (if mortality rates are low). These dynamics suggest that competition among bears within Great Smoky Mountains may be great, particularly during years of poor food production. All of these propensities are supported by my findings of high population density (see Chapter 2), male-dominated mortality outside the Park (see chapter 3), relatively small weights and body size (see chapter 5), and large fall movements during years of poor mast production (see chapter 3).

Limitations of this investigation made it difficult to draw definitive conclusions regarding the exact timing and magnitude of dispersal. Similar to Clevenger and Pelton (1990), this study suffered from small sample sizes due to the tendency of females with yearlings to move when approached and logistical constraints of performing fieldwork in

the backcountry with limited access. I was only able to radiocollar one family group, and both yearlings dropped their collars within 5 months of den emergence. Of 8 other bears radiocollared during summer trapping because they weighed less than 22.5 kg, only 5 were verified as yearlings from tooth aging. Additionally, I lost contact with 5 yearlings that did not drop their collars. Inclement weather and scheduling difficulties reduced the number of telemetry flights that I was able to conduct, which resulted in long gaps between successive locations of the yearlings. Consequently, large movements by individual bears could have kept them from being detected and being recorded as dispersal events. Radiocollar failure is a stronger possibility, most likely due to battery charge drainage. The expandable radiocollars used were untested and had shorter range and weaker batteries than the collars used for adult bears.

Telemetry data were bolstered by data from distances between recaptures. The large sample size (590 distances) and long time frame (1968 – 1998) of these data made them robust compared to the deficiencies of the telemetry data. A shortcoming of the recapture data was the categorical nature of the distances. Bears only could be captured at specific sites that had fixed distances among them. Bears that moved completely out of the study areas were not sampled. Even so, there were over 125 trapsites at which bears could be caught, providing ample opportunity over the 31 years of the study for even relatively rare movements to be detected. Overall, I believe that the two analyses complemented each other and gave a reasonable portrayal of the dynamics involved with bear dispersal in Great Smoky Mountains National Park.

CHAPTER V

WEIGHTS AND MORPHOMETRICS

Introduction

The relationship between animal weights and body sizes and the environment has been investigated in several species of animals. Positive correlations between habitat quality and animal size and weight have been documented in cottontail rabbits (*Sylvilagus floridanus*) (Pelton 1970), muskrats (*Ondatra zibethicus*) (Dozier 1950, Schacher and Pelton 1976), Gunnison's prairie dogs (*Cynomys gunnisoni*) (Rayor 1985), white-tailed deer (*Odocoileus virginianus*) (Richie 1969), and black bears (Rogers 1976, McLean 1991). Moreover, Eason (1995) demonstrated that black bear weights and morphometrics varied by ecoregion province in the United States and that bears within the same population varied in size from year to year. He concluded that these bears might be responding to differences in habitat quality and available energy. However, Eason (1995) also found an inverse relationship between mast failure and black bear weights and morphometrics in GSMNP; bear weights increased in the summer following a mast failure. Upon closer inspection, he found that the average age of captured bears also had increased and speculated that large dominant bears had remained in GSMNP while smaller less dominant bears were forced to leave in search of food. Consequently, many subdominant bears likely were killed by hunters or in collisions with automobiles.

Because of findings like these, investigations of phenotypic plasticity in bears may best be conducted in a single population that has been studied over a long period.

The black bear database for GSMNP includes weights and morphometric measurements since the early 1970s. Information on bear litter sizes and hard mast data also are available. These data afford an opportunity to investigate the relationships among hard mast production (available energy), bear weights and morphometrics, and reproduction (cub production). Black bear weights and body sizes should correlate positively with hard mast production of the preceding fall, except in cases of extreme mast shortage. During these times of food scarcity, based on Eason's (1995) findings, an inverse relationship between weights and morphometrics and fall mast would be expected. Litter sizes should be greatest in years following those with large female body size (better nutrition). If relationships exist among hard mast production, bear weights and morphometrics, and cub production, equations may be derived that allow for prediction of desired parameters. For example, because cub production is difficult and costly to document, managers would benefit from having an equation that predicted cub production based on mast production the previous fall or female weights.

The specific objectives of this study were to determine if black bear weights and morphometrics vary among years within GSMNP and whether they correlate with hard mast production or bear litter sizes.

Study Area

The study area was located within the northwest portion of GSMNP and was designated as the Tennessee study area (TNSA). This study area comprised less than 20% of the total land area of GSMNP and was placed to represent the wide array of cover types occupied by bears within the Park. The TNSA was originally established in 1967 and has been continuously sampled, in various forms, to the present. Because of differing objectives for the studies that have been conducted on the TNSA, specific study areas, traplines, and trapsites have changed slightly over the years. The general location for all of these studies has been the area stretching eastward from the northwestern boundary of GSMNP to highway 441 and northward from the North Carolina-Tennessee border to the northern boundary of the Park (Fig. 2.1). From 1989 - 1998, during which sampling was standardized, the TNSA totaled 358 km^2.

Methods

I used capture information from 544 black bears trapped during summers 1967 to 1998 to determine if weights and morphometrics of bears within GSMNP varied from year to year. Project personnel captured and handled bears by means of standard techniques (Johnson and Pelton 1980) every summer from May to August. Personnel immobilized bears by injection of a 10:5:1 mixture of Ketaset (ketamine hydrochloride, Aveco Co., Inc., Fort Dodge IA), Rompun (xylazine hydrochloride, Rugby Laboratories, Inc., Rockville Center, NY), and Carbocaine-V (mepivicaine hydrochloride, Sterling Drug Inc., McPherson, KS) (KRC). Personnel administered KRC intramuscularly via jab

pole syringe or blowpipe dart at 1 cc per 25 kg of bear weight. Once immobilized, bears were treated with opthalmic ointment to moisturize eyes and triple anitbiotic to disinfect minor cuts and wounds. Personnel subsequently measured (to the nearest 1 cm), weighed (to the nearest lb.), ear-tagged, and lip-tattoed all bears. Also, a premolar tooth was extracted for aging by use of cementum annuli (Willey 1974) and blood and hair samples were collected for future serological and genetic analyses unrelated to this project. Personnel revived bears by injection of Yohimbine (Lloyd Laboratories, Shenandoah, Iowa) and recorded all data on standard University of Tennessee bear capture forms.

In addition to weight, the seven morphometrics that I investigated were: chest girth, forearm girth, head length, head width, neck girth, shoulder height, and total body length (Table 5.1). Because of the propensity for black bears to undergo significant intra-year variation in body size, I restricted my analyses to bears caught during the summer (May – August). Additionally, I included adults (bears ≥ 4 years old) only to reduce size differences associated with growth as much as possible (Eason 1995). To increase sample sizes and account for sexual dimorphism between males and females, I employed a sexual correction factor, or zwitter. Following the technique of Schnell et al. (1985) and Eason (1995), I calculated the female zwitter as one-half of the weighted proportional difference between males and females for each parameter divided by the weighted proportional difference. For males, I calculated the zwitter as one-half of the weighted proportional difference divided by 100 + the weighted proportional difference. I then increased the female parameters with the value of female zwitter and decreased the male parameters by the value of the male zwitter. See Eason (1995) for details of this

Table 5.1. Description of weight and morphometric parameters taken for morphometric study of adult black bears in Great Smoky Mountains National Park, summers 1976-1998.

Morphometric	Code	Description
Chest Girth	CG	-the circumference of the chest (directly behind the front legs) on the exhale
Forearm Girth	FG	-the circumference of the thickest part of the forearm
Head Length	HL	-distance from tip of bone in nose to back of sagittal crest
Head Width	HW	-the circumference of the head over the zygomatic arches
Neck Girth	NG	-the circumference of the neck
Height at Shoulder	HAS	-distance from tip of most distal metacarpal to top of scapula
Total Body Length	TBL	-distance from the tip of the nose, along the backbone, to the tip of the most distal tail vertebra
Weight	WT	-total body weight of bear taken with hanging scale

procedure. I grouped bears by year of capture (Table 5.2) and compared their weights and morphometrics using analysis of variance (SAS Inst., Inc. 1990). I employed a Bonferonni-type adjustment to correct alpha levels for multiple univariate tests, lowering significance thresholds from $\alpha = 0.05$ to 0.00625. I tested the following null and research hypotheses:

H_0: Black bear weights and morphometrics do not vary among years.

H_R: Black bear weights and morphometrics vary significantly among years.

More specifically, I tested the hypothesis that weights and morphometrics increased following years of mast scarcity, presumably because of dominant individuals hoarding available resources and causing subdominants to leave the Park in search of food. I combined bear weights and morphometrics into 2 categories, those among years immediately following mast failures and those during non-failure years (Table 5.2). I used mast data gathered by GSMNP personnel employing the Whitehead survey method (Whitehead 1969) from 1979 – 1998 (GSMNP unpubl. data). Data were collected on white oak species (white oak and chestnut oak) and red oak species (northern red oak, scarlet oak), and were summarized by each type and overall (Table 5.3). I defined years of mast failure as those with a total oak (white and red oak species combined) Whitehead index < 2.0. I used analysis of variance (SAS Inst., Inc. 1990) to perform this analysis, set significance levels to the Bonferonni-adjusted level of $\alpha = 0.00625$, and tested the following null and research hypotheses:

Table 5.2. Hard mast status and sample sizes of black bear weights and morphometrics used in morphometric analyses in Great Smoky Mountains National Park, 1976 - 1998.

Year		Mast Status	Sample Size*
1976		---	26
1977		---	25
1978		---	---
1979		Normal	15
1980		Normal	26
1981		Normal	25
1982		Normal	---
1983		Post Failure	18
1984		Normal	22
1985		Normal	14
1986		Normal	13
1987		Normal	34
1988		Normal	20
1989		Normal	41
1990		Normal	25
1991		Normal	39
1992		Post Failure	31
1993		Post Failure	21
1994		Normal	31
1995		Normal	52
1996		Normal	33
1997		Normal	42
1998		Post Failure	36
	Total	Normal	483
		Post Failure	106
	Grand Total	Combined	589

*Years with sample size < 10 were excluded from analyses; sample sizes varied slightly among parameters analyzed – values shown are maximums.

Table 5.3. Whitehead Index hard mast survey results from Great Smoky Mountains National Park, 1979 - 1998.

	Whitehead Index		
Year	White Oaks	Red Oaks	Total Oak
1979	3.84	3.48	3.66
1980	0.50	4.77	2.99
1981	4.13	2.66	3.29
1982*	0.65	2.14	1.62
1983	---	---	---
1984	---	---	---
1985	3.08	2.60	2.83
1986	2.82	3.46	3.17
1987	3.39	3.34	3.36
1988	3.22	3.33	3.30
1989	1.77	3.62	3.03
1990	2.28	2.74	2.52
1991*	1.54	1.46	1.49
1992*	1.65	2.05	1.88
1993	0.27	3.31	2.19
1994	1.34	2.62	2.04
1995	1.99	4.60	3.63
1996	4.05	2.22	2.94
1997*	0.46	2.88	1.98
1998	1.81	3.84	3.19

*Years with total oak indices < 2.0 were classified as mast failures.

H_0: Black bear weights and morphometrics do not change following years of mast failure.

H_R: Black bear weights and morphometrics increase following years of mast failure.

Additionally, I conducted a multivariate canonical correlation analysis in SAS (proc CANCORR) to investigate the relationships of hard mast production and reproductive output with variations in bear weights and morphometrics. I considered any correlations at or below the $\alpha = 0.05$ level to be significant. I tested the following null and research hypotheses:

H_0: Black bear weights and morphometrics do not correlate with hard mast production and average litter size.

H_R: Black bear weights and morphometrics correlate with hard mast production and average litter size.

Results

After correction for sexual dimorphism and combining sexes to increase sample sizes, all 8 weight and morphometric parameters varied significantly through time from 1976 – 1998 ($P = 0.0001$ for each parameter) (Table 5.4). When grouped by mast failure status, the average values of 6 of the 8 weight and morphometric parameters did not differ in years following mast failures compared to other years (Table 5.5); however, height at shoulder and head length were significantly smaller ($P = 0.0020$ and $P = 0.0001$, respectively). The canonical correlation analysis between the weight and morphometric

Table 5.4. Average weight (kg) and morphometric* (cm) parameters from black bears captured in Great Smoky Mountains National Park, summers 1976 – 1998. Data from years with sample sizes smaller than 10 were omitted.

	WT		TBL		CG		HAS		NG		HL		HW		FG	
Year	Mean	Std.	Mean	Std.	Mean	Std.	Mean	Std.	Mean	Std.	Mean	Std.	Mean	Std.	Mean	Std.
1976	63.6	14.1	152.3	8.8	85.2	8.2	78.3	6.7	52.9	5.4	32.6	1.3	27.2	2.1	31.4	2.6
1977	72.0	19.3	155.3	7.9	87.7	11.7	79.9	5.7	54.3	7.8	32.4	1.7	26.8	3.4	32.2	3.0
1978	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
1979	57.5	18.2	147.5	12.0	80.6	9.5	80.6	5.5	49.5	6.2	32.3	1.8	23.9	3.5	29.3	3.8
1980	69.3	15.4	153.2	9.5	87.1	8.9	78.3	7.4	54.8	9.8	32.4	1.5	27.1	2.6	32.3	2.6
1981	62.9	9.9	150.6	9.7	78.9	6.1	75.6	4.8	49.9	4.0	32.2	1.6	27.2	1.9	30.7	2.3
1982	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
1983	57.8	13.8	156.7	11.0	78.2	11.4	84.2	6.0	50.5	5.8	33.1	2.0	27.3	2.9	32.0	3.6
1984	58.4	16.6	155.5	11.6	76.3	10.0	81.8	7.6	48.3	6.4	32.1	1.9	26.1	2.8	30.0	3.5
1985	58.2	17.0	154.2	12.7	73.7	7.5	81.8	5.9	47.5	6.3	32.6	1.9	28.4	2.8	28.6	3.2
1986	60.4	11.7	151.0	8.6	77.6	6.0	79.1	3.2	50.1	4.6	31.1	1.0	24.7	1.5	32.0	2.0
1987	68.8	13.3	162.3	8.9	88.0	7.6	86.5	5.2	55.2	4.7	33.8	2.0	31.1	3.7	33.8	3.8
1988	61.5	16.1	158.2	11.5	84.0	8.2	84.1	8.3	52.4	6.1	32.8	2.4	26.2	3.1	31.4	4.0
1989	63.7	20.6	153.5	12.4	81.1	11.7	78.9	8.4	51.7	8.4	32.7	2.0	27.5	3.1	30.6	4.1
1990	57.3	20.5	152.0	14.1	78.8	13.1	79.8	10.6	49.5	8.8	32.7	2.3	27.3	3.3	29.8	4.7
1991	62.2	18.7	154.6	13.4	81.2	10.8	82.4	7.8	52.0	7.2	31.9	2.7	27.2	2.9	31.3	3.9
1992	67.5	22.6	159.7	10.8	85.0	11.6	85.5	6.3	53.4	7.9	32.1	2.8	27.0	3.3	32.0	3.4
1993	68.9	9.3	161.3	9.2	85.1	6.0	82.5	7.9	52.9	5.4	32.7	1.4	28.0	3.4	32.3	2.2
1994	74.8	17.5	152.4	9.6	85.8	10.2	78.8	7.4	52.9	6.3	32.1	2.0	28.1	3.9	31.8	3.1
1995	75.5	18.8	157.2	10.0	87.2	10.4	80.3	5.1	53.4	6.7	33.0	2.0	28.5	3.3	31.8	3.5
1996	71.7	22.3	156.0	12.3	89.3	13.8	81.2	5.8	54.4	7.4	32.5	2.3	28.7	2.8	30.2	4.7
1997	74.4	11.8	151.6	6.8	89.2	7.9	80.4	4.2	56.5	6.4	27.1	2.1	29.0	4.2	32.2	2.8
1998	61.2	20.1	147.1	10.7	79.6	11.8	65.9	4.9	50.7	8.4	25.9	1.8	27.2	4.1	27.3	3.6
Mean	65.5	28.1	154.7	15.4	83.5	15.7	79.3	10.2	52.2	10.8	31.5	3.7	27.7	4.3	31.0	5.1

*See table 5.1 for weight and morphometric codes.

Table 5.5. Comparison of average weight (kg) and morphometric* (cm) parameters from black bears captured after years of mast failure and non-failure in Great Smoky Mountains National Park, summers 1976 – 1998. Data from years with sample sizes smaller than 10 were omitted.

	WT		TBL		CG		HAS		NG		HL		HW		FG	
Year†	Mean	Std.	Mean	Std.	Mean	Std.	Mean	Std.	Mean	Std.	Mean	Std.	Mean	Std.	Mean	Std.
NF	66.4	18.2	154.4	11.2	83.8	10.8	80.7	7.1	52.5	7.2	32.0	2.6	27.8	3.5	31.3	3.8
F	64.3	18.3	155.2	12.0	82.0	11.0	78.0	10.7	51.9	7.4	30.3	3.8	27.3	3.5	30.5	4.0
Diff.	2.1	---	-0.8	---	1.8	---	2.7ϕ	---	0.6	---	1.7ϕ	---	0.5	---	0.8	---

*See table 5.1 for weight and morphometric codes.
†F = years following failures in mast production (1983, 1992, 1993, 1998); NF = years following non-failure mast production (all other years).
ϕParameter values differed significantly between years of non-failure and failure at $\alpha = 0.00625$.

and hard mast/reproduction parameters yielded non-significant results. The weight and morphometric parameters exhibited many high correlations among themselves: chest girth and neck girth, chest girth and weight, neck girth and weight, and height shoulder and total body length all had correlation coefficients > 0.8000 (Table 5.6). Among the hard mast/reproductive parameters, both the red and white oak indices exhibited high correlation coefficients with the total oak index (Table 5.6). None of the weight and morphometric and hard mast/reproduction parameters were highly correlated (all correlation coefficients < 0.5000) (Table 5.6). Additionally, none of the 4 canonical variables derived from the weight and morphometric and hard mast/reproduction parameters were significantly correlated (P = 0.5074, 0.7283, 0.9371, and 0.8744 for the first, second, third, and fourth canonical variables, respectively), indicating that multivariate correlations among the parameters did not exist at significant levels.

Discussion

Although significant fluctuations occurred through time, I could discern no clear pattern of temporal variation in the weight and morphometric parameters investigated in this study. I believed that three factors accounted for this finding. The first factor related to influence of rare measurements. Sample sizes in this study ranged from 13 – 52, with most > 20 (Table 5.2). Even so, the average weight and morphometric parameters were sensitive to large and small values, which may have influenced the yearly fluctuations in the parameters. Extreme small values could have resulted from delayed growth in subdominant bears or starvation in general, whereas extreme large values were associated

Table 5.6. Correlations among hard mast indices and weights, morphometrics, and litter sizes the following year for black bears in Great Smoky Mountains National Park, summers 1976 - 1998*.

Variable†	CG	FG	HL	HW	NG	HAS	TBL	WT	Red Oak	White Oak	Total Oak	Litter Size
CG	1.0000											
FG	0.3763	1.0000										
HL	-0.1887	-0.0409	1.0000									
HW	0.6670	0.3586	0.0552	1.0000								
NG	0.9464	0.5231	-0.3427	0.6454	1.0000							
HAS	0.2401	0.4885	-0.0409	0.3586	0.2936	1.0000						
TBL	0.3912	0.5103	0.4911	0.4323	0.3479	0.8440	1.0000					
WT	0.8763	0.3411	-0.2757	0.5754	0.8005	-0.0638	0.1590	1.0000				
Red Oak	-0.0047	-0.4844	0.2601	0.1357	-0.1425	-0.4978	-0.3535	-0.0475	1.0000			
White Oak	0.2790	0.2061	-0.3992	-0.0374	0.4493	0.0732	-0.0514	0.0273	-0.0633	1.0000		
Total Oak	0.1680	-0.2679	-0.0631	0.0626	0.1716	-0.3418	-0.3327	-0.0415	0.7396	0.6192	1.0000	
Litter Size	0.2889	-0.0377	-0.2447	-0.0581	0.2313	-0.0907	-0.0337	0.3480	-0.2470	-0.1241	-0.2575	1.0000

*Note: the canonical correlation analysis showed that none of the correlations were significant at the $\alpha = 0.05$ level.
†see Table 5.1 for weight and morphometric codes; Red Oak = red oak Whitehead mast index, White Oak = white oak Whitehead mast index, Total Oak = combined red and white oak Whitehead mast index, and Litter Size = average bear litter size.

with rare, naturally large bears with access to abundant foods. Removal of only one or two extreme values from certain years was enough to significantly alter the results. Because I believed that all of the data were accurate and genuine, I did not include any of the reduced data set analyses in the final results.

The second factor that I believed contributed to the lack of pattern in bear weights and morphometrics was individual variation within and between years. Black bears normally experience wide fluctuations in their body weight throughout the year. Bears emerge from hibernation with low fat stores; contend with relatively low food levels through the spring and early summer, when weight and body size may continue to decrease; begin to fatten up in the late summer; enter hyperphagy in the fall in preparation for winter denning; and then fast throughout the winter until they emerge again in the spring. Given these dynamics, I believed it best to analyze weights and morphometrics in the summer when bears should have had time to recover from winter dormancy, but had not entered hyperphagy. The use of weights and morphometrics collected in the spring would have introduced variation related to reproductive status, whereas the use of fall weights and morphometrics would have introduced variation associated with individual bears' ability to find fall foods and convert them into fat stores. Additionally, individual bears might be affected in various ways, depending upon their experience, dominance, and luck in finding adequate food during mast failures. Inexperienced and subdominant bears probably experience greater shifts in weights and morphometrics in relation to mast availability, with starvation playing a significant role in the dynamics of these individuals during severe shortages of food.

Although I restricted my analyses to bears 4.5 years and older, these individuals continued to grow. McLean (1991) found that in GSMNP the growth of females leveled off, whereas males continued to grow throughout adulthood. Additionally, McLean (1991) showed that females did not attain their greatest weight until age 9 for wild bears and 12 for panhandler bears. Such continued growth could have confounded my analyses if significant numbers of older bears were sampled in some years compared to others. Mean age varied by year (range 5.6 – 9.0 years; $P = 0.0048$), although there was broad overlap in years with similar mean ages. Mean ages did not vary by mast failure status (normal = 7.1 and failure = 7.2 years; $P = 0.6153$), and the only parameter that correlated significantly with average ages was neck girth ($P = 0.0050$; corr. coef. = 0.63). No other weight and morphometric variables correlated significantly with age after Bonferonni adjustment of critical values. Consequently, I concluded that any affects of age on body size were slight, particularly for the analysis of weights and morphometrics following mast failures.

The final factor affecting the weights and morphometrics of bears in this study was alternate food sources. Numerous studies have documented the importance of fall hard mast for black bears in the southern Appalachians (Beeman and Pelton 1980, Eagle and Pelton 1983, Beringer 1986, Garner 1986, Seibert 1989, McLean 1991), but few (Eiler 1981, Warburton 1984, Inman 1997) have documented the importance of soft mast. Kasbohm (1995) showed that bears in Shenandoah National Park shifted feeding to abundant soft mast species favored after elimination of hard mast-bearing trees by the gypsy moth. Similarly, I hypothesized that the availability of large amounts of squawroot

(*Conopholis americana*), huckleberry (*Vaccinium* spp.), blackberry (*Rubus* spp.), grape (*Vitis* spp.), and other soft mast-bearing species in GSMNP affected bear weights and morphometrics to the extent that hard mast availability, by itself, did not account for changes in bear weights and morphometrics.

When grouped together across all mast failure events, average weights and morphometrics did tend to be smaller following years of mast failure. However, when inspected individually, this pattern did not hold consistently for each event. In fact, the only year in which weights and morphometrics dropped after a mast failure was 1998, when every parameter decreased noticeably from the previous year. The weights and morphometrics in other years following mast failures showed similar levels (1983 and 1992) or slightly higher levels (1993) than those did in previous years. The magnitude of the decrease in 1998 was great enough to override the relatively weak differences in other years following mast failures and caused the combined average values to be lower than those in years of non-failure mast production. These results indicated that the bear popoulation in GSMNP might have reacted to individual mast failures differently, depending on the circumstances. One mast failure was followed by a sharp decrease in bear weights and body size, but 2 other failures resulted in minimal changes.

The overall results of this investigation did not support earlier findings (Eason 1995) that weights and morphometrics increased following years of mast failure. I did find the same curious trend of increasing weights and body size following the 1992 mast failure. However, the increases calculated in this study were much smaller and less dramatic than those originally found by Eason (1995). The main factor accounting for

this difference was my development of individualized sexual correction factors for bears in GSMNP compared to Eason's (1995) use of sexual correction factors computed from bear populations located across the southeastern United States. The net result of these different correction factors was that parameters calculated from them in this study were significantly smaller ($p=0.0001$ for all parameters) and more precise than those calculated by Eason (1995). This difference was particularly true for females, which made up a large proportion of captures in 1993 (helping to raise the average weight and body size of bears in that year). Even so, the point is moot because incorporation of other mast failure events resulted in a net decrease in most weight and morphometric parameters. These data indicated that if, as Eason (1995) hypothesized, dominant bears force other bears outside of GSMNP during mast failures, such behavior is not evidenced by consistently increasing weights and morphometrics following years of severe mast failure. Instead, on average, weights and body sizes tended to decrease slightly following mast shortages.

The lack of a consistent pattern in weights and morphometrics following mast failures, in conjunction with the lack of correlation between weights and morphometrics and hard mast/reproductive parameters, indicated that bears in GSMNP were able to ameliorate the effects of hard mast shortage. The most likely alternate source of food was soft mast. Black bears in GSMNP seem to have evolved behavioral plasticity that allows them to exploit continually changing food sources. The most obvious and well-documented adaptation is increased movements during the fall to forage on highly dispersed food sources. The results of this study suggested that the use of soft mast abundant in spring and summer might be another equally important adaptation. Future

studies seeking to understand the dynamics of bear populations should investigate the long-term relationship of soft mast and other non-hard mast foods on bear nutrition and reproduction. The influence of rare bears with extremely small or large body sizes should be accounted for in any such analyses.

CHAPTER VI

SUMMARY

1. The long-term database compiled on black bears in GSMNP from 1968 to the 1998 afforded a unique opportunity to study the population ecology of bears. The database consisted of summer trapping and winter denwork on bears in the TNSA from 1967 to 1998 and in the NCSA from 1994 to 1998. Overall, the database contained > 2,500 bear captures and was formed from numerous smaller studies; each conducted for 2 to 4 years. Trapping efforts did not become totally consistent on the TNSA until 1989 when 8 traplines were permanently established. Consequently, I focused most of my analyses on the time period 1989 – 1998, concentrating comparisons between the study areas to the period 1994 – 1998. I bolstered certain analyses with data from the entire period, when appropriate.

2. I estimated population abundance on both study areas using 3 closed models (Lincoln/Petersen, Bailey's Binomial, and back dating) and 1 open model (Jolly/Seber). I generated abundance estimates for the years 1989 – 1998 on the TNSA and 1994 – 1998 on the NCSA. I used mark-recapture data from summer trapping in the Lincoln/Petersen, back dating, and Jolly/Seber models. For Bailey's Binomial model, I used mark-resight data from summer trapping and remote cameras.

3. The use of remote cameras to resight black bears for population size estimation proved useful and efficient. Overall on both study areas, 1,011 sighting

opportunities over 3,346 camera nights produced 400 pictures, 368 (92%) of bears and 32 (8%) of non-target animals. Thirty-three percent (330/1,011) of the sighting opportunities resulted in useable bear pictures, with the number of camera nights per useable bear picture averaging 10.1. I did not detect any trap response in relation to placement of camera sites at or away from trap sites.

4. Incorporation of remote camera resight data into Bailey's Binomial model yielded abundance estimates for 1996 on the TNSA and 1996 – 1998 on the NCSA. The estimates for the NCSA averaged 218 bears, and the estimate for the TNSA was 165 bears. Resight probabilities were high, ranging from 25 – 45%; consequently, lower and upper 95% confidence limits were relatively small, ranging from 19 – 82% of the abundance estimates. Abundance estimates generated from remote camera resight data tended to be lower than estimates from other models.

5. Lincoln/Peterson estimates ranged from 377 – 521 bears on the NCSA and 311 – 647 bears on the TNSA. Resight probabilities were low (4 – 21%), resulting in lower and upper 95% confidence limits that were large (ranging from 33 – 120% of the abundance estimates). Lincoln/Petersen estimates were consistently higher than those from other models were.

6. Back dating estimates ranged from 178 – 229 bears on the NCSA and 178 – 262 bears on the TNSA. Because back dating estimates were generated from simple population reconstruction, no resight probabilities or confidence intervals could be calculated. Overall, back dating estimates seemed to adequately portray the minimum number of bears known to be alive on each study area.

7. I selected model A as the best fitting model from program JOLLY and generated abundance estimates from it for both study areas. Estimates ranged from 258 – 856 bears on the NCSA and 167 – 411 bears on the TNSA. Resight probabilities varied markedly, but tended to be low (range 5 – 40%). Because of the relatively low resight rates and the increased number of parameters needed to generate estimates as compared to closed models, the lower and upper 95% confidence limits were large for the Jolly/Seber estimates (ranging from 28 – 327% of the abundance estimates). Jolly/Seber estimates fluctuated greatly from year to year, but tended to be higher than most other estimates.

8. I estimated various potential effective study area sizes by taking the cumulative area circumscribed from buffering all trapsites with radii whose length approximated the average distance bears would travel to trapsites. I calculated potential buffer radii from 4 separate measures: mean home range radius, mean distance between recaptures, mean distance between radio-isotope tagged scats and nearest trapsite, and distance between telemetry locations and point of capture. I concluded that the mean home range radius best approximated the effective study area and used it to calculate areas for density estimation. Additionally, I used the overall average radius from all measures to generate the area of use around trapsites for study area delineation. Based on these distances, study areas totaled 357.7 and 400.5 km^2 for the TNSA and NCSA, respectively and effective study areas totaled 252 and 274 km^2 for the NCSA and TNSA, respectively.

9. I calculated densities by dividing abundance estimates by the effective study

area size for each study area. To improve robustness and reduce bias, I excluded all abundance estimates that were generated with resight probabilities less than 10%. Density estimates from the Lincoln-Petersen model averaged 1.63 and 1.77 bears/km^2 on the NCSA and TNSA, respectively. Density estimates from Bailey's Binomial model averaged 0.79 and 0.65 bears/km^2 on the NCSA and TNSA, respectively. Density estimates from the back dating model averaged 0.73 and 0.93 bears/km^2 on the NCSA and TNSA, respectively. Density estimates from the Jolly-Seber model averaged 0.94 and 1.20 bears/km^2 on the NCSA and TNSA, respectively. Overall, density estimates generated in this study were higher than those previously calculated in GSMNP, except for estimates by Coley (1995), which were much higher than those found in this study.

10. I concluded that the Lincoln/Petersen results likely were affected by significant negative trap response and, consequently, overestimated bear density. Bailey's Binomial results tended to be lower than even the back dating estimates, indicating that they may have suffered from positive trap response; however, the frequency of marked bears photographed at sites adjacent to and offset from trapsites did not differ. Jolly-Seber results were most robust, but lacked precision because of low resight rates. Back dating results only indicated the minimum number of bears alive, but generated density estimates for every year of the study, allowing analysis of trend information.

11. Bait station indices that were adjusted for trap saturation correlated significantly with the back dating density estimates, but did not correlate significantly with density estimates from any other model. Bait station indices accounted for 64% of

the variation in the back dating estimates, indicating that they did track changes in the minimum number of bears known to be alive on each study area.

12. A limiting factor on the precision and accuracy of estimates generated during this study was study area size and shape. Because of historical and logistic constraints, trapsites were placed along traplines that were dispersed throughout large sections of GSMNP. Consequently, study areas were large and elongated, and could not be saturated with trapsites. The result was low resight probabilities and large confidence intervals. Future population estimation studies conducted in GSMNP should address this major limitation.

13. Sex ratios (males: female) were skewed toward males on the NCSA (1.53:1) and TNSA (1.48:1). I concluded that the greater proportion of males was due to their larger home ranges and more frequent contact with trapsites. Also, sex ratios fluctuated from year to year on both study areas in correspondence to breeding synchrony as females with cubs encountered trapsites at lower rates.

14. Mean age of female bears was significantly older than that of males. Females averaged 5.99 and 6.23 years of age on the NCSA and TNSA, respectively. Males averaged 4.59 and 4.25 years of age on the NCSA and TNSA, respectively. The relatively high average age for both sexes in conjunction with the presence of many older bears was consistent with high survival estimates that suggested a lightly exploited population.

15. Mean weight of bears in GSMNP was relatively light compared to other black bear populations, and, as expected male bears were significantly heavier than

female bears. Females averaged 42.5 kg on the NCSA and 43.0 kg on the TNSA, whereas males averaged 65.0 on the NCSA and 65.9 kg on the TNSA.

16. Average litter size of female bears was higher on the TNSA than the NCSA, most likely due to small sample sizes. Mean litter size was 2.1 cubs on the NCSA and 2.7 cubs on the TNSA. Overall, mean litter sizes were comparable to those documented in other studies in the southern Appalachians. Yearly fluctuations in litter size indicated that most bears were in breeding synchrony, producing cubs in 1994 and 1996.

17. I estimated adult female survival from telemetry data collected on radio-collared bears. Overall survival rates were 0.931 on the NCSA and 0.905 on the TNSA. Six bears died of natural causes, 5 bears were legally harvested, and 1 bear died of unknown causes. Mortality rates tended to be low during most years and increased sharply during years of mast failure.

18. I compared the population characteristics estimated in this study between the NCSA and TNSA from 1994 to 1998. Density, as estimated by the back dating model, was the only parameter that varied significantly between the 2 study areas, averaging approximately 25% lower on the NCSA than the TNSA. The 3 other models had reduced sample sizes and large variances that prohibited robust analyses. Consequently, I concluded that, even though the other model estimates did not differ between the study areas, the back dating estimates reflected true differences in density. Differences in habitat quality likely accounted for the differences in density between the 2 study areas. Because of its predominantly northward facing slopes the TNSA had higher percentages of cover types containing white oaks. Conversely, the predominantly southward facing

slopes of the NCSA favored cover types with more red oaks, but fewer white oaks. I hypothesized that the lower tanin content of white oak acorns made them more palatable to bears and increased the carrying capacity of the TNSA compared to the NCSA.

19. I investigated the dispersal dynamics of black bears in GSMNP with 2 techniques. In the first technique, I placed expandable radiocollars on yearling black bears and tracked their movements via aerial telemetry flights. In the second technique, I examined the distances traveled between captures of bears. Both techniques indicated that yearling bears did not disperse and that male bears dispersed more often than females. The few bears that did disperse tended to do so when they were subadults, or 2.5 to 3.5 years old. The delayed dispersal documented in this study was consistent with the hypothesis that bears in high density populations defer dispersal until sufficient body size is attained to compete with adult males. Additionally, the low frequency of dispersal events found in this study, particularly for females, suggests that population range expansion in the southern Appalachian Mountains would be slow and unlikely across wide areas of unsuitable habitat.

20. Collaring and tracking of yearling bears proved difficult during this study. Because of logistic constraints and propensity of female bears with yearlings to move when approached during winter denning, I had to abandon hopes of radiocollaring entire family groups of females with yearlings. Instead, I resorted to collaring bears that weighed less than 22.5 kg during summer trapping. Seven of ten bears radiocollared in this manner were confirmed as yearlings from tooth sectioning. Aerial tracking of yearlings was difficult because of weather conditions, early dropping of expandable

collars, and loss of signal.

21. Distances between recaptures of bears varied significantly among age classes and between sexes. Bears in the subadult age class exhibited the largest distance between captures (average = 2,642 m), whereas yearlings exhibited the smallest distance (average = 328 m). Male bears moved further between recaptures than female bears did. Six females traveled further than an average female home range diameter, with the greatest distance documented being 15,445 m. Twelve males traveled further than an average male home range diameter, with the greatest distance equaling 26,434 m.

22. Weights and morphometrics (external body size measurements) of bears in GSMNP varied significantly among years from 1976 to 1998. I investigated the influence of hard mast production on these fluctuations, but could find no clear pattern. When grouped by hard mast failure status, 7 of 8 weight and morphometric parameters were smaller in years following mast failures compared to other years. However, this pattern was driven by a single mast failure that resulted in large decreases in bear weights and body size. During the other 2 mast failures, weights and morphometrics stayed approximately equal to previous years or increased slightly. No multivariate correlations existed among weight and morphometric parameters and hard mast/reproduction parameters.

23. Removal of only a few extreme measurements resulted in significant changes to average annual weight and morphometric values. Therefore, use of these parameters may be problematic in population studies. Based on results of this study, if used, sample sizes of weight and morphometric parameters should be large (> 50).

24. Results from this investigation of weights and morphometrics did not support Eason's (1995) findings that bear body size and weight increases after fall hard mast failures, presumably because dominant bears drive other bears out of GSMNP and do not suffer increased mortality rates associated with leaving the sanctuary of the Park. Weights and morphometrics did increase slightly after 1 mast failure event, but this pattern did not hold for the other 2 mast failure events. Bears in GSMNP seemed to respond to mast failures in different ways; consequently, weights and morphometrics showed no clear pattern following failures.

25. Based on the lack of correlation between weights and morphometrics and hard mast found in this study, I concluded that alternate food sources played a significant role in the nutrition of bears in GSMNP. The most evident alternate food source was soft mast in the form of grapes, huckleberries, blueberries, cherries, and blackberries. Squawroot and insects were other food sources potentially important to black bears. I hypothesized that exploitation of these food sources during the spring and summer affected black bear weights and morphometrics and confounded correlations with hard mast indices. Future studies seeking to understand bear population dynamics in the southern Appalachians should incorporate soft mast and other non-hard mast food sources into their investigations.

26. Overall, this study found no evidence to support the contention that poaching or other mortality factors accounted for differences in density between the 2 study areas. Instead, habitat characteristics most likely were the cause. Bears in GSMNP seemed to respond to higher habitat quality by increasing density, with severe mast failures affecting

bears proportionally on each study area. The implications of such dynamics include long-term unpredictability of major mortality events and potential for density of bears to increase significantly during long periods of adequate nutrition. During this study, these effects resulted in years of mortality spikes, usually in the form of legal harvest, followed by marked breeding synchrony that produced large pulses of cubs. Recruitment of these individuals into the population during consecutive years of decent mast production allowed populations to quickly rebound from mortality events and reach some of the highest densities recorded for black bears. Park officials should be aware of this tendency toward high density and take appropriate precautions with visitor and resource management.

LITERATURE CITED

Alt, G. L. 1978. Dispersal patterns of black bears in northeastern Pennsylvania – a preliminary report. Eastern Workshop Black Bear Manage. and Res. 4:186-198.

Bacon, E. S. 1973. Investigation on perception and behavior of the American black bear (*Ursus americanus*). Ph.D. dissertation, Univ. Tennessee. 161 pp.

Beeman, D. K., and M. R. Pelton. 1978. The effects of the immobilizing drugs phencyclidine hydrochloride and etorphine hydrochloride on blood parameters of black bears. Eastern Workshop Black Bear Manage. and Res. 4:125-137.

_____. 1981. Serum and whole blood parameters of black bears in the Great Smoky Mountains National Park. M.S. thesis, Univ. Tennessee. 84 pp.

Beeman, L. E. 1971. Seasonal food habits of the black bear (*Ursus americanus*) in the Smoky Mountains of Tennessee and North Carolina. M.S. thesis, Univ. Tennessee. 62 pp.

_____. 1975. Population characteristics, movements, and activities of the black bear (*Ursus americanus*) in the Great Smoky Mountains National Park. Ph.D. dissertation, Univ. Tennessee. 218 pp.

_____. and M. R. Pelton. 1977. Seasonal foods and feeding ecology of black bears in the Smoky Mountains. Int. Conf. Bear Res. Manage. 4:141-147.

Beringer, J. J. 1986. Habitat use and response to roads by black bears in Harmon Den, Pisgah National Forest, North Carolina. M.S. thesis, Univ. Tennessee. 103 pp.

Bowman, J. L., M. J. Chamberlain, B. D. Leopold, and H. A. Jacobson. 1996. An evaluation of two censusing techniques to estimate black bear population size on White River National Wildlife Refuge, Arkansas. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies. 50:614-621.

Bunnell, F. L. and D. E. N. Tait. 1981. Population dynamics of bears – implications. pp. 75-98 *In* C. W. Fowler and T. D. Smith, eds. Dynamics of large mammal populations. John Wiley and Sons, New York, NY.

Burst, T. L. 1979. An analysis of trees marked by black bears in the Great Smoky Mountains National Park. M.S. thesis, Univ. Tennessee. 80 pp.

_____. and M. R. Pelton. 1983. Black bear mark trees in the Smoky Mountains. Int. Conf. Bear Res. Manage. 5:45-53.

Carr, P. C. 1983. Habitat utilization and seasonal movements of black bears in the Great Smoky Mountains National Park. M.S. thesis, Univ. Tennessee. 95 pp.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons. N.Y. 234 pp.

Chapman, D. G. 1951. Some properties of the hypergeometric distribution with applications to zoological censuses. Univ. Calif. Publ. Stat. 1:131-160.

Clark, J. D. 1991. Ecology of two black bear populations in the interior highlands of Arkansas. Ph.D. dissertation, Univ. Arkansas. 228 pp.

Clevenger, A. P., and M. R. Pelton. 1990. Pre and post breakup movements and space use of black bear family groups in Cherokee National Forest, Tennessee. Int. Conf. Bear Res. Manage. 8:289-295.

Coley, A. B. 1995. Population dynamics of black bears in Great Smoky Mountains National Park. M.S. thesis, Univ. Tennessee. 180 pp.

Cook, W. J., and M. R. Pelton. 1978. Selected infectious and prasitic diseases of black bears in the Great Smoky Mountains National Park. Eastern Workshop Black Bear Manage. Res. 4:120-124.

_____. 1982. Biochemical, hematological, and pathological observations of black bears in the Smoky Mountains. M.S. thesis, Univ. Tennessee. 89 pp.

Daugherty, J. P., D. K. Beeman, and M. R. Pelton. 1979. Analysis of the electrophoretic pattern of nonspecific esterases of black bear serum. J. Tenn. Acad. Sci. 54:128-131.

Dice, L. R. 1938. Some census methods for mammals. J. Wildl. Manage. 2:119-130.

_____. 1941. Methods for estimating populations of mammals. J. Wildl. Manage. 5:398-407.

Dickson, R. R. 1960. Climates of the states: Tennessee. U. S. Dept. Commerce, Weather Bureau. Climatology fo the U. S., No. 60-40. 16 pp.

Dozier, H. L. 1950. Muskrat trapping on the Montezuma National Wildlife Refuge, New York, 1943-1948. J. Wildl. Manage. 14:403-412.

Eagar, D. C. 1977. Radioisotope feces tagging as a population estimator of black bear (*Ursus americanus*) density in the Great Smoky Mountains National Park. M.S. thesis, Univ. Tennessee. 89 pp.

_____. and M. R. Pelton. 1978. Panhandler black bears in the Great Smoky Mountains National Park: methods and ethological research. Eastern Workshop Black Bear Manage. Res. 4:138-154.

Eagle, T. C. 1979. Foods of black bears in the Great Smoky Mountains National Park. M.S. thesis, Univ. Tennessee. 104 pp.

_____. and M. R. Pelton. 1983. Seasonal nutrition of black bears in the Great Smoky Mountains National Park. Int. Conf. Bear Res. Manage. 5:94-101.

Eason, T. H. 1995. Weights and morphometrics of black bears in the southeastern United States. M.S. thesis, Univ. Tennessee. 132 pp.

Eiler, J. H. 1981. Reproductive biology of black bears in the Smoky Mountains of Tennessee. M.S. thesis, Univ. Tennessee. 117 pp.

_____., W. G. Wathen, and M. R. Pelton. 1988. Reproduction in black bears in the southern Appalachian mountains. J. Wildl. Manage. 53:353-360.

Eubanks, A. L. 1976. Movements and activities of the black bear (*Ursus americanus*) in the Great Smoky Mountains National Park. M.S. thesis, Univ. Tennessee. 83 pp.

_____., J. Sparks, and M. R. Pelton. 1976. Selected chemical analyses of black bear serum. J. Tenn. Acad. Sci. 51:29-31.

Fenneman, N. M. 1938. Physiography of eastern United States. McGraw-Hill Book Co., New York and London. 714 pp.

Garner, N. P. 1986. Seasonal movements, habitat selection, and food habits of black bears (Ursus americanus) in Shenandoah National Park, Virginia. M.S. thesis, Virginia Polytech. Inst. and State Univ. 104 pp.

Garris, R. S. 1983. Habitat utilization and movement ecology of black bears in Cherokee National Forest. M.S. thesis, Univ. Tennessee. 98 pp.

Garshelis, D. L. 1978. Movement ecology and activity of black bears in the Great Smoky Mountains National Park. M.S. thesis, Univ. Tennessee. 117.

_____. and M. R. Pelton. 1978. Assessment of the use of telemetric motion sensors for monitoring activity behavior in black bears. Eastern Workshop Black Bear Manage. Res. 4:220-226.

_____. and M. R. Pelton. 1980. Activity of black bears in the Great Smoky Mountains National Park. J. Mammal. 61:8-19.

_____. and M. R. Pelton. 1981. Movements of black bears in the Great Smoky Mountains National Park. J. Wildl. Manage. 45:912-925.

_____., H. B. Quigley, C. R. Villarrubia, and M. R. Pelton. 1982. Assessment of telemetric motion sensors for studies of activity. Can. J. Zool. 60:1800-1805.

_____., H. B. Quigley, C. R. Villarrubia, and M. R. Pelton. 1983. Diel movements of black bears in the Southern Appalachians. Int. Conf. Bear Res. Manage. 5:11-19.

_____. 1991. Monitoring effects of harvest on black bear populations in North America: a review and evaluation of techniques. Eastern Workshop Black Bear Res. Manage. 10:120-144.

_____. 1994. Density-dependent population regulation of black bears. pp. 3-14 In M. Taylor, ed. Density dependent population regulation in black, brown, and polar bears. Int. Conf. Bear. Res. Manage. Monogr. Series No. 3. 43 pp.

Golden, M. S. 1974. Forest vegetation and site relationships in the central portion of the Great Smoky Mountains National Park. Ph.D. dissertation, Univ. Tennessee. 275 pp.

Grogan, R. G. and F. G. Lindzey. 1999. Estimating population size of a low-density black bear population using capture-resight. URSUS 11:117-122.

Hastings, B. C., M. R. Pelton and P. A. Petko-Seus. 1987. Use of backcountry visitor areas by problem bears in Great Smoky Mountains National Park. Proc. Conf. on Science Nat'l. Parks. Vol. 2. Wildl. Manage. and Habitat. pp. 82-88.

Hellgren, E. C. and M. R. Vaughan. 1989. Range dynamics of black bears in Great Dismal Swamp, Virginia-North Carolina. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 44:268-278.

Herrmann, R. and S. Bratton. 1977. Great Smoky Mountains National Park as a biosphere reserve: a research/monitoring perspective. NPS Manage. Rep. No. 23. 38 pp.

Inman, R. M. 1997. Caloric production of black bear foods in Great Smoky Mountains National Park. M.S. thesis, Univ. Tennessee. 163 pp.

Johnson, K. G. 1978. Den ecology of black bears (*Ursus americanus*) in Great Smoky Mountains National Park. M.S. thesis, Univ. Tennessee. 107 pp.

_____. and M. R. Pelton. 1979. Denning behavior of black bears in the Great Smoky Mountains National Park. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies. 33:239-249.

_____. and M. R. Pelton. 1980*a*. Den ecology of black bears in Tennessee. Eastern Workshop Black Bear Manage. Res. 5:198-204.

_____. and M. R. Pelton. 1980*b*. Prebaiting and snaring techniques for black bears. Wildl. Soc. Bull. 8:46-54.

_____. and M. R. Pelton. 1981. Selection and availability of dens for black bears in the Great Smoky Mountains National Park. J. Wildl. Manage. 45:11-119.

_____. and M. R. Pelton. 1983. Population estimates and indices for black bears in Southern Appalachian mountains. *In*: pp. 103-133. D. Carlock, D. Conley, O. Collins, K. Johnson, S. Johnson, and M. R. Pelton, cooperators. The Tri-State Black Bear Study Report. TWRA Tech. Report No. 85-9. 285 pp.

Jordan, R. H. 1979. An observational study of the American black bear (*Ursus americanus*). Ph.D. dissertation, Univ. Tennessee. 169 pp.

Kasbohm, J. W., M. R. Vaughan, and J. G. Kraus. 1995. Food habits and nutrition of black bears during a gypsy moth infestation. Can. J. Zool. 73:1771-1775.

King, P. B. and A. Stupka. 1950. The Great Smoky Mountains – their geology and natural history. Sci. Month. 71:31-43.

_____., P. B. Neuman, and J. B. Hadley. 1968. Geology of the Great Smoky Mountains National Park, Tennessee and North Carolina. Geol. Sur. Prof. Pap. 587. 23 pp.

Krebs, C. J. 1998. Ecological methodology. 2nd Edition. Benjamin Cummings, Menlo Park, CA. 620 pp.

Lafollette, J. D. 1974. Some aspects of the history of the black bear (*Ursus americanus*) in the Great Smoky Mountains. M.S. thesis, Univ. Tennessee. 149 pp.

Linzey, A. V. and D. N. Linzey. 1971. Mammals of the Great Smoky Mountains National Park. University of Tennessee Press, Knoxville. 114 pp.

Mace, R. D., S. C. Minta, T. L. Manley, and K. E. Aune. 1993. Estimating grizzly bear population size using camera sightings. Wildl. Soc. Bull. 21:74-83.

MacKenzie, M. D. 1991. Vegetation map of Great Smoky Mountains National Park based on LANDSAT thematic mapper data: accuracy assessment and numeric descriptions of vegetation types. Report submitted to Southeastern Region of the National Park Service. Uplands Field Laboratory, Gatlinburg, TN.

_____. 1993. The vegetation of Great Smoky Mountains National Park: past present, and future. Ph.D. dissertation, Univ. Tennessee. 154 pp.

Manly, B. F. J. 1984. Obtaining confidence limits on parameters of the Jolly-Seber model for capture-recapture data. Biometrics 40:749-758.

Marcum, L. C. 1974. An evaluation of radioactive feces-tagging as a technique for determining population densities of the black bear (*Ursus americanus*) in the Great Smoky Mountains National Park. M.S. thesis, Univ. Tennessee. 95 pp.

Martorello, D. A., T. H. Eason, and M. R. Pelton. 2001. A sighting technique using cameras to estimate population size of black bears. Wildl. Soc. Bull. 29:560-567.

Matson, G., L. Van Daele, E. Goodwin, L. Aumiller, H. Reynolds, and H. Hristienko. 1993. A laboratory manual for cementum age determination of Alaska brown bear first premolar teeth. AK Dept. Fish and Game, Div. Wildl. Conserv. 52 pp.

Matthews, S. K. 1977. The seasonal, altitudinal, and vegetational incidence of black bear scats in Great Smoky Mountains National Park. M.S. thesis, Univ. Tennessee. 89 pp.

McLean, P. K. 1991. The demographic and morphological characteristics of black bears in the Smoky Mountains. Ph.D. dissertation, Univ. Tennessee. 156 pp.

_____. and M. R. Pelton. 1991. Some demographic comparisons of wild and panhandler bears in the Smoky Mountains. Int. Conf. Bear Res. Manage. 8:105-112

_____. 1994. Estimates of population density and growth of black bears in the Smoky Mountains. Int. Conf. Bear Res. Manage. 9:253-261.

Mohr, C. O. and W. A. Stumpf. 1966. Comparison of methods for calculating areas of animal activity. J. Wildl. Manage. 30:293-304.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildl. Monogr. 62. 135 pp.

Pedersen, J. A. 1995. The influence of ecological and temporal factors on trap response by black bears in Great Smoky Mountains National Park. M.S. thesis, Univ. Tennessee. 114 pp.

Pelikan, J. 1967. The estimation of population density in small mammals. pp. 267-273. *In* K. Petrusewicz, ed. Secondary productivity of terrestrial ecosystems; principles and methods - Proceedings of the working meeting Secondary Productivity of Terrestrial Ecosystems. Polish Academy of Sciences, Warsaw.

_____. 1968. Testing and elimination of the edge effect in trapping small mammals. pp. 57-61. *In* K. Petrusewicz and L. Ryszkowski, eds. Proceedings of IBP meeting on secondary productivity in small mammal populations. Polish Scientific Publishers, Warsaw.

_____. 1971. Calculated densities of small mammals in relation to quadrat size. Ann. Zool. Fennici 8:3-6.

Pelton, M. R. 1970. Weights and measurements of Georgia cottontails and an ecological principle. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies. 24:268-277.

_____. and L. E. Beeman. 1975. A synopsis of population studies of the black bear in the Great Smoky Mountains National Park. Proc. S. Reg. Am. Assoc. Zoos and Zoological Parks. Knoxville, TN. pp 43-48.

_____. and L. C. Marcum. 1975. The potential use of radioisotopes for determining densities of black bear and other carnivores. pp. 221-236. In Proc. Pred. Symp. R. 1. Phillips and C. Jonkel, eds. Montana Forest and Conservation Expt. Sta., Univ. of Montana Missoula. 268 pp.

_____. and F. T. van Manen. 1996. Benefits and pitfalls of long-term research: a case study of black bears in Great Smoky Mountains National Park. Wildl. Soc. Bull. 24:443-450.

Petko-Seus, P. A. 1985. Knowledge and attitudes of campers toward black bears in Great Smoky Mountains National Park. M.S. thesis, Univ. Tennessee. 173 pp.

_____., B. C. Hastings, W. E. Hammitt, and M. R. Pelton. 1985. Public attitudes toward collars and ear markers on wildlife. Wildl. Soc. Bull. 13:283-286.

_____. and M. R. Pelton. 1986. Backpacker bear knowledge in Great Smoky Mountains National Park. Proc. 4th Conf. Social Research in Nat'l. Parks and Wildland Areas.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. J. Wildl. Manage. 53:7-15.

_____, J. D. Nichols, C. Browne, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildl. Monogr. 107. 97 pp.

Pozzanghera, S. A., B. D. Nolan, Jr., and M. R. Pelton. 1986. Inducing salvation in immobilized black bears for the purpose of estrogen analysis. Eastern Workshop Black Bear Manage. Res. 8:168-173.

_____. 1990. The reproductive biology, winter dormancy and denning physiology of black bears in Great Smoky Mountains National Park. M.S. thesis, Univ. Tennessee. 126 pp.

Quigley, H. B., D. L. Garshelis, M. R. Pelton, C. I. Taylor, and C. R. Villarrubia. 1979. Use of activity monitors in telemetry studies. Proc. 2nd Internat. Conf. on Wildlife Biotelemetry. 2:48-56.

_____. 1982. Activity patterns, movement ecology, and habitat utilization of black bears in the Great Smoky Mountains National Park, Tennessee. M.S. thesis, Univ. Tennessee. 140 pp.

Rayor, L. S. 1985. Effects of habitat quality on growth, age of first reproduction, and dispersal in Gunnison's prairie dogs (*Cynomys gunnisoni*). Can. J. Zool. 63:2835-2840.

Reynolds, D. G. and J. J. Beecham. 1980. Home range activities and reproduction of black bears in west-central Idaho. Int. Conf. Bear Res. Manage. 4:181-190.

Richie, W. F. 1969. Regional differences in weight and antler measurements of Illinois deer. Trans. Illinois State Acad. Sci. 62:189-197.

Rogers, L. 1976. Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. Proc. N. Am. Wildl. Conf. 41:431-438.

_____. 1987a. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. Wildl. Monogr. 97. 72 pp.

_____. 1987b. Factors influencing dispersal in the black bear. In B. D. Chepko-Sade and Z. T. Halpin, eds. Mammalian dispersal patterns. Univ. Chicago Press. Chicago, IL. 342 pp.

SAS Institute, Inc. 1990. SAS/STAT User's Guide, Version 6, 4th edition, Volumes 1 and 2. SAS Institute Inc., Cary, NC.

Schacher, W. H. and M. R. Pelton. 1976. Sex ratios, morphology and condition parameters of muskrats in East Tennessee. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies. 30:594-608.

Schnell, D. S., M. E. Douglas, and D. J. Hough. 1985. Sexual dimorphism in spotted dolphins (*Stenella attenuata*) in the eastern tropical Pacific Ocean. Mar. Mamm. Sci. 1:1-14.

Schwartz, C. C. and A. W. Franzmann. 1992. Dispersal and survival of subadult black bears from the Kenai Peninsula, Alaska. J. Wildl. Manage. 56:426-431.

Seber, G. A. F. 1970. The effects of trap-response on tag-recapture estimates. Biometriks 26:13-22.

_____. 1982. The estimation of animal abundance and related parameters. 2nd ed. MacMillan Publ. Inc. New York, New York. 654 pp.

Seibert, S. G. 1989. Black bear habitat use and response to roads on Pisgah National Forest, North Carolina. M.S. thesis, Univ. Tennessee. 144 pp.

Shanks, R. E. 1954*a*. Climates of the Great Smoky Mountains. Ecology 35:354-361.

_____. 1954*b*. Reference list of native plants in the Great Smoky Mountains. Botany Dept., Univ. Tennessee, Knoxville. 14 pp., mimeo.

Shields, W. M. 1987. Dispersal and mating systems: investigating their causal connections. In B. D. Chepko-Sade and Z. T. Halpin, eds. Mammalian dispersal patterns. Univ. Chicago Press. Chicago, IL. 342 pp.

Smith, K. G. and J. D. Clark. 1994. Black bears in Arkansas: characteristics of a successful translocation. J. Mammal. 75:309-320.

Soil Survey. 1945. Sevier County. U. S. Dept. of Agriculture, Univ. Tenn. Agric. Exp. Sta., and Tenn. Valley Auth. 203 pp.

_____. 1953. Blount County. U. S. Dept. of Agriculture, Univ. Tenn. Agric. Exp. Sta., and Tenn. Valley Auth. 119 pp.

Stephens, L. A. 1969. A comparison of climatic elements at four elevations in the Great Smoky Mountains National Park. M.S. thesis, Univ. Tennessee. 119 pp.

Stickel, L. F. 1954. A comparison of certain methods of measuring ranges of small mammals. J. Mammal. 35:1-15.

Stiver, W. H. 1991. Population dynamics and movements of problem black bears in Great Smoky Mountains National Park. M.S. thesis, Univ. Tennessee. 134 pp.

Stupka, A. 1960. Great Smoky Mountains National Park natural history handbook. No. 5. U. S. Govt. Printing Office, Washington, D. C. 75 pp.

Tate, J. 1979. Aggression in human-bear interactions: The influences of setting. Proc. 2nd Conf. on Sci. Research in National Parks. Vol. 16. NCIS. Springfield, VA.

_____. 1983*a*. A profile of panhandling black bears in the Great Smoky Mountains National Park. M.S. thesis, Univ. Tennessee. 190 pp.

_____. 1983*b*. Human-bear interactions: profile and perspective. In: A. H. Katcher and A. N. beck (eds). New perspectives on our lives with companion animals. Univ. Of Penn. Press. Phil., PA. Pp. 205-218.

Thornthwaite, C. W. 1948. An approach toward a rational classification of climate. Geog. Rev. 38:55-94.

van Manen, F. T. 1994. Black bear habitat use in Great Smoky Mountains National Park. Ph.D. dissertation, Univ. Tennessee. 212 pp.

Villarubia, C. R. 1982. Movement ecology and habitat utilization of black bears in Cherokee National Forest, Tennessee. M.S. thesis, Univ. Tennessee. 159 pp.

Warburton, G. S. 1984. An analysis of a black bear sanctuary in western North Carolina. M.S. thesis, North Carolina State Univ. 121 pp.

Wathen, W. G. 1983. Reproduction and denning of black bears in the Great Smoky Mountains. M.S. thesis, Univ. Tennessee. 135 pp.

_____., K. G. Johnson, and M. R. Pelton. 1983. Characteristics of black bear dens in the southern Appalachian region. Int. Conf. Bear Res. Manage. 6:119-127.

_____. and M. R. Pelton. 1984. Characteristics of black bear cubs in the Southern Appalachians. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies. 38:62-69.

White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, LA 8787-NERP, Los Alamos, N.M. 235 pp.

Whitehead, C. J. 1969. Oak mast yields on wildlife management areas in Tennessee. Unpubl. Report. TN Game and Fish Commission, Nashville. 11 pp.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr. 26:1-80.

Willey, C. H. 1974. Aging black bears from first premolar tooth sections. J. Wildl. Manage. 38:97-100.

APPENDICES

Appendix A. Results of regression analysis on all years of captures versus first year of captures only for back dating estimates in Great Smoky Mountains National Park.

Model: MODEL1
Dependent Variable: OVERALL

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Prob>F
Model	1	3107.48538	3107.48538	67.031	0.0001
Error	7	324.51462	46.35923		
C Total	8	3432.00000			

Root MSE	6.80876	R-square	0.9054
Dep Mean	201.00000	Adj R-sq	0.8919
C.V.	3.38744		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	T for H0: Parameter=0	Prob > |T|
INTERCEP	1	151.115010	6.50200466	23.241	0.0001
FIRSTYR	1	0.953216	0.11642736	8.187	0.0001

Figure A.1. SAS output for regression of all years of captures versus first year of captures only for back dating estimates of black bear population size in Great Smoky Mountains National Park, summers 1989 – 1998.

Appendix B. Summary of distance distributions used in calculating the effective study area size for black bears in Great Smoky Mountains National Park.

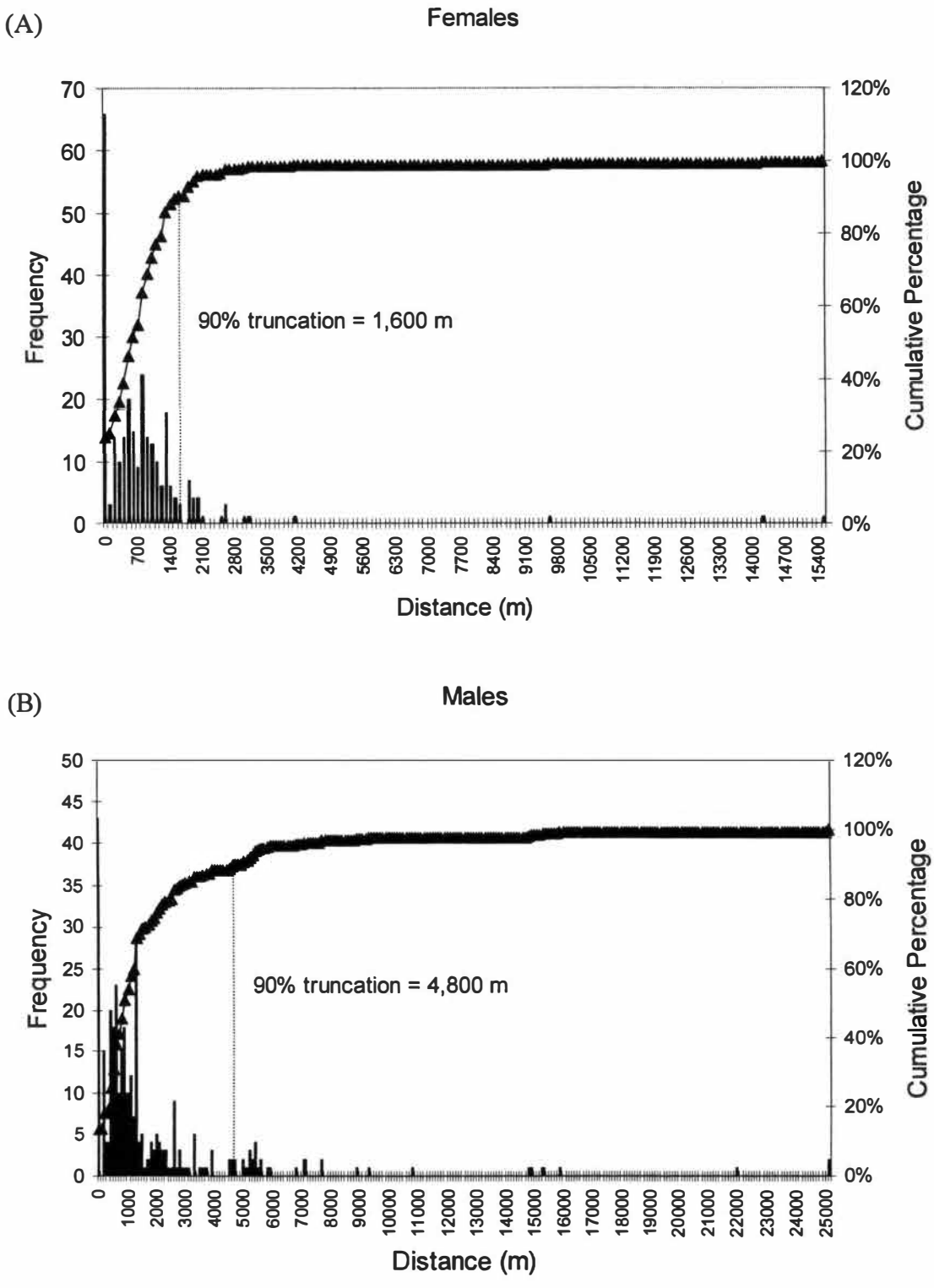


Figure B.1. Distribution of distances between capture locations of (A) female and (B) male bears in Great Smoky Mountains National Park, summers 1967 – 1998. Distributions were truncated at 90% for input into effective study area delineation.

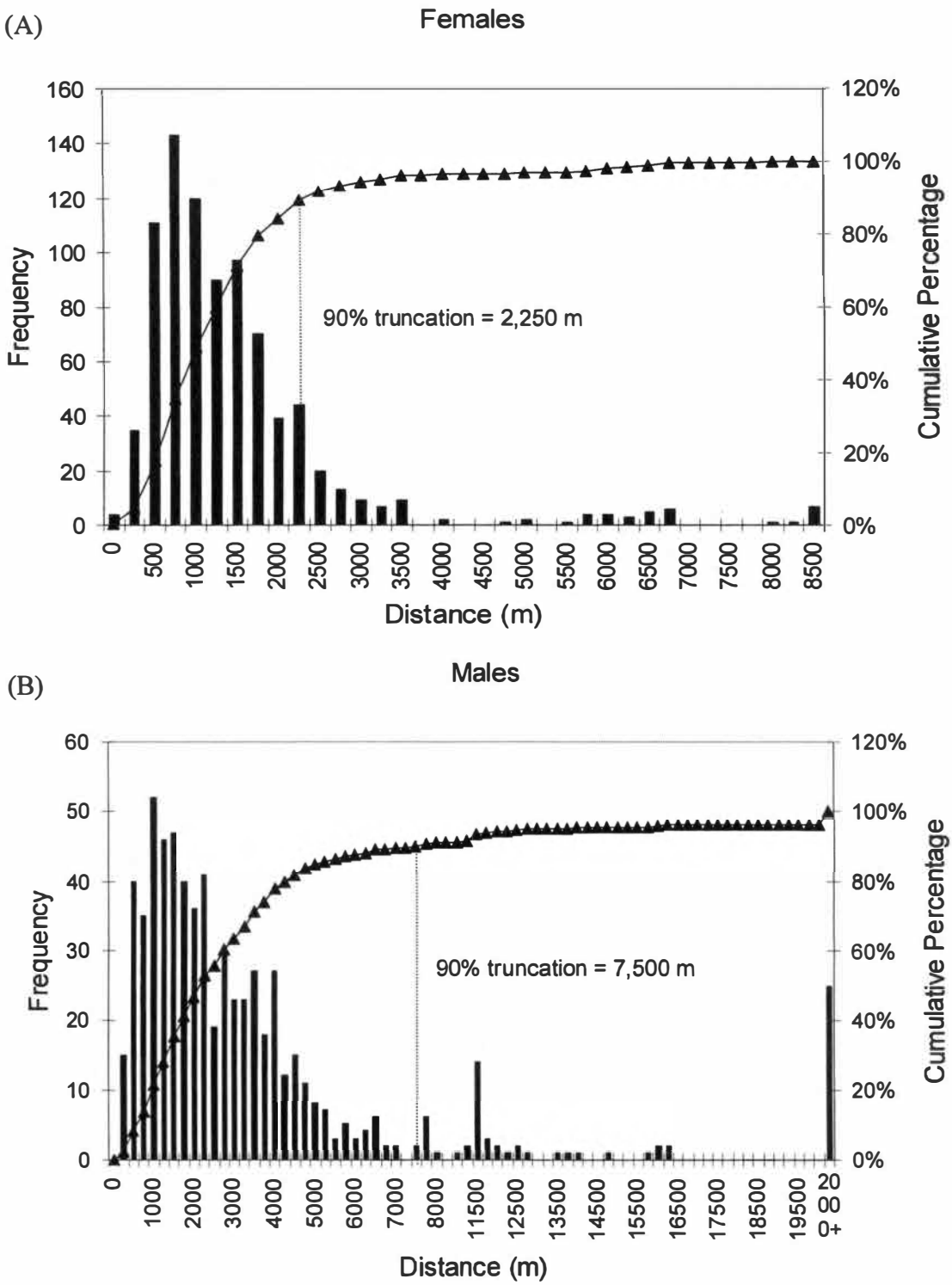


Figure B.2. Distribution of distances between telemetry locations and point of capture for (A) female and (B) male bears in Great Smoky Mountains National Park, summers 1967 – 1998. Distributions were truncated at 90% for input into effective study area delineation.

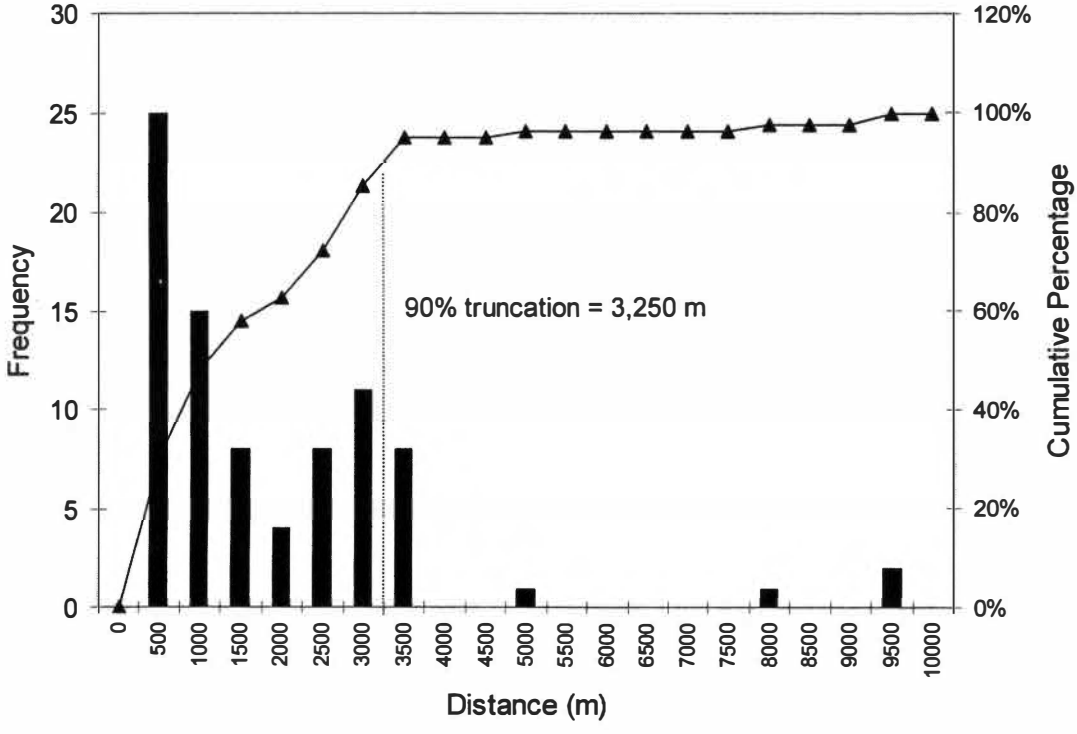


Figure B.3. Distribution of distances between radio-isotope tagged scats and point of capture for bears in Great Smoky Mountains National Park, summers 1974 – 1975 (adapted from Eubanks 1976). Distribution was truncated at 90% for input into effective study area delineation.

Appendix C. Summary of correlations between and among the bait station index and density estimates for black bears in Great Smoky Mountains National Park.

Table C.1. Correlation coefficients and significance values (below) among the adjusted bait station index and various density estimates for black bears in Great Smoky Mountains National Park, summers 1989-1998.

Variable	Back Dating	Lincoln - Petersen	Jolly - Seber	Bailey's Binomial	Adj. Bait Station
Back Dating	1.00 0.0000				
Lincoln/Petersen	0.44 0.2787	1.00 0.0000			
Jolly/Seber	0.03 0.9344	0.26 0.6742	1.00 0.0000		
Bailey's Binomial	0.18 0.8236	0.52 0.6509	-0.81 0.4039	1.00 0.0000	
Adjusted Bait Station	0.64 0.0097*	-0.01 0.9827	-0.47 0.2007	0.44 0.5599	1.00 0.0000

*Statistically significant correlation.

VITA

Thomas Hunter Eason was born on April 11, 1970 in Arlington, Virginia. He graduated from James Madison High School in Vienna, Virginia in 1988. He then attended Virginia Polytechnic Institute and State University (VA Tech), where he received a Bachelor of Science degree in Forestry and Wildlife in May 1992. He received the Master's of Science degree in Wildlife and Fisheries Science at the University of Tennessee, Knoxville (UTK) in December 1995. Thomas performed his doctoral research in the Department of Ecology at the UTK from 1994 – 1998. In 1999, Thomas moved to Florida and has served as the Bear Management Section Leader for the Florida Fish and Wildlife Conservation Commission since then. He was awarded the Doctor of Philosophy degree at the UTK in May 2002. Thomas is married to Danielle Marie Unger and resides in Tallahassee, Florida.